United States
Department of
Agriculture

Forest Service

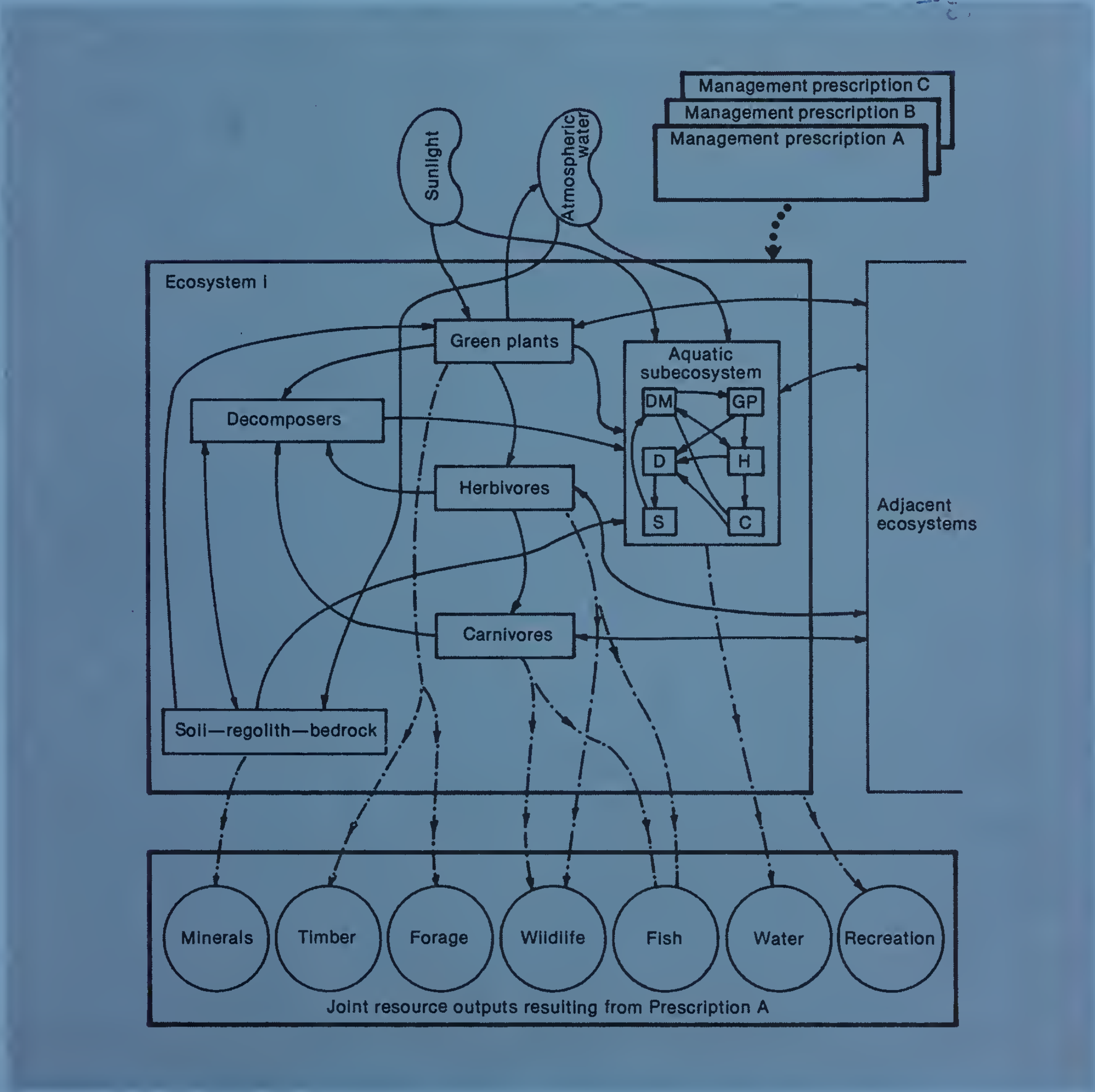
**Rocky Mountain
Forest and Range
Experiment Station**

Fort Collins,
Colorado 80526

**General Technical
Report RM-105**

Estimation of Animal Production Numbers for National Assessments and Appraisals

Stephen A. Miller



Acknowledgments

To prepare this report, information concerning techniques in use was solicited from several state officials. The author greatly appreciates the contributions of the following agencies and individuals in enabling those elements of the review to be completed:

- Alabama Game and Fish Division
  - James E. Keeler, Chief, Wildlife Research
- Alaska Department of Fish and Game
- Georgia Game and Fish Division
  - Joe Kurz, Assistant Chief, Game Management Section
- Hawaii Division of Forestry and Wildlife
  - Timothy Sutterfield, Wildlife Biologist
- Iowa Conservation Commission
  - James M. Kienzler, Wildlife Research Biologist
- Kansas Fish and Game
- Maine Department of Inland Fisheries and Wildlife
  - Frederick B. Hurley, Jr., Wildlife Resources Planner
- Michigan Department of Natural Resources
  - Keith L. Heezen, Federal Aid Coordinator
- Missouri Department of Conservation
  - Bill T. Crawford, Superintendent, Wildlife Research Section
- Montana Department of Fish and Game
  - Dr. John P. Weigand, Chief, Research Bureau
- Nebraska Game and Parks Commission
  - Norm Dey, Administrative Assistant
- Nevada Department of Wildlife
  - George K. Tsukamoto, Chief, Game Division
- New Hampshire Fish and Game Department
  - Theodore W. Walski
- New York State Department of Environmental Conservation
  - Peggy R. Sauer, Supervising Wildlife Biologist
- North Carolina Wildlife Resources Commission
  - George E. Smith, Assistant Chief, Division of Game
- North Dakota Game and Fish Department
  - Paul T. Schadewald, Federal Aid Coordinator
- Ohio Division of Wildlife
  - Robert W. Donohoe, Supervisor, Forest Wildlife Project
  - Gregory L. Mountz, Supervisor, Survey and Inventory Section
  - Robert J. Stoll, Wildlife Biologist
- Pennsylvania Fish Commission
  - Richard A. Snyder, Chief, Fisheries Management Section
- South Carolina Wildlife and Marine Resources Department
- Texas Parks and Wildlife Department
  - Craig A. McMahan, Director, Programs, Planning
- Utah Division of Wildlife Resources
  - John Salevurakis, Federal Aid Coordinator
- Wisconsin Department of Natural Resources
  - James R. Huntoon, Administrator, Division of Resource Management
  - Don Thompson
- Wyoming Game and Fish Department

Special thanks go to Dr. Kenneth P. Burnham for his assistance in analyzing the Ohio line-transect data for ruffed grouse and for his continued encouragement and advice in developing this report.

This project would not have been completed without the financial assistance of the Office of Biological Services, USDI Fish and Wildlife Service.

USDA Forest Service
General Technical Report RM-105

February 1984

Estimation of Animal Production Numbers for National Assessments and Appraisals

Stephen A. Miller, Wildlife Biologist[1]
Maryland Department of Natural Resources

Abstract

Population inventory methods and associated data are best applied in national assessments of wildlife and fish in conjunction with analytical approaches which utilize estimates of the production capability of the supporting habitat. Current knowledge of estimating animal population numbers is contrasted with current practice. Problems in using available population data as input for national assessments are reviewed.

---

[1] *Publication developed while author was wildlife biologist serving with the Fish and Wildlife Service, U.S. Department of the Interior, on IPA assignment from the State of Maryland.*

Contents

Estimation of Animal Production Numbers for National Assessments and Appraisals

Stephen A. Miller

NATIONAL ASSESSMENT IMPLICATIONS

Agencies are increasingly expected to conduct wildlife and fish resource assessments and inventories as part of a broader multiresource approach. This trend is reinforced by two basic factors (Hirsch et al. 1979). First, because wildlife and fish resources compete with some other uses of the land, such as crop production, livestock grazing, and urban expansion, information about wildlife and fish must be comparable to information about these other resources in order to evaluate resource production tradeoffs resulting from various land management strategies. Second, multiple-resource inventories are more efficient than parallel, but separate, functional efforts.

A conceptual framework for assessing wildlife and fish resources should be based on the production capability of the habitat which supports a species or population. Using this approach, the habitat is described by the population level of a species either occupying or capable of being supported in that habitat. This approach also would help to greatly improve the ability to predict the quantitative effects of habitat changes on animal populations (Schweitzer et al. 1981).

There are basically two methods for determining the supportive capability of this habitat. The first uses knowledge of individual species/habitat relationships to develop models which predict the overall suitability of the habitat according to an appropriate rating scheme. This method interprets the potential production capability of the habitat. The second method uses statistical techniques to determine those habitat variables which are correlated with the abundance and distribution of a species. A prior knowledge of species/habitat relationships is not required with this approach. The resultant models are designed to predict the production capability of the habitat in terms of the population numbers expected in the area.

Both methods require data on wildlife population numbers. To calibrate the habitat suitability index derived by the first method to the actual wildlife populations requires data on species abundance. The second method also requires data base related to species abundance and distribution.

Population estimation methods and associated inventory data appear to be best used in national assessments of wildlife and fish in conjunction with the analytical approaches described above. The individual states can and should provide much of this data.

Anyone who solicits or develops input regarding animal populations for national assessments should be aware of several problems with current and historical inventory information presently available. First, population density information is quite limited in scope. Thus, in turn, limits the number of species which can be considered in a national assessment. Second, much of the quantitative information on populations generally lack estimates of error. Without a standard error, there is no way to know how reliable the estimates are. Third, various animal population surveys have used less than optimal survey designs and techniques. The resulting population density estimates may be less reliable than estimates obtained using the newer techniques and analytical capabilities now available. Some of these are examined and discussed in this report.

INTRODUCTION

Davis and Winstead (1980) said that the methods used for estimating numbers of animals have evolved conceptually from simple counts to complex sampling programs and mathematical models, and that the technical calculations involved have progressed from pencil and paper to computer. There are many approaches to estimating populations, not all of which have been developed.

This review has three main objectives. The first is to present current methods for estimating wildlife populations focusing, where possible, on the following (Eberhardt 1978a):

(1) Mechanics of the method (field and mathematical aspects).
(2) Assumptions about the conditions under which observations are made.
(3) Presentation of the formal model used with the method.
(4) Such statistical aspects of the estimator as bias, efficiency, and robustness to failure of assumptions.

The second objective is to contrast the methods available for estimating animal populations with the methods actually in use. Literature was reviewed on completed research by the Divisions of Wildlife and

Fishery Ecology-Research and the Office of Cooperative Units within the U.S. Fish and Wildlife Service. Documentation from state projects done with federal aid also was reviewed. Documentation was solicited from the states for those projects which use techniques for estimating absolute or relative density as an integral part of the investigations.

The third objective is to evaluate the role of the methods for estimating populations and the role of the available data generated by these methods in national assessments of wildlife and fish.

COMPLETE ENUMERATION

The most direct way to determine the number of animals in a population is to count them all. Such a complete enumeration is called a census. Two types of censuses are recognized: (1) spatial censuses, in which a count is made of all the animals in a specified area at a specified time, and (2) temporal censuses, in which a count is made of all animals passing a particular place during a specified period of time (Overton 1971).

Territory-Mapping Method

One census technique is territory-mapping. This spatial method works on territorial species (i.e., occupy an ecological, if not a behavioral territory) which can be readily observed within their territories.

Standards for applying the territory-mapping method to bird census work were developed by the International Bird Census Committee (1970). This international standard was designed to alleviate problems of comparing the results of bird censuses obtained by different workers, in different habitats, or in different regions or countries. The Committee's report contains a discussion of the recommended procedural guidelines and data analysis processes.

Researchers using the territory-mapping method should state the population (or community) density as the number of stationary males (mapped territories) per 10 ha or per square kilometer.

The Michigan Department of Natural Resources, in cooperation with the USDA Forest Service, USDI Fish and Wildlife Service, the Michigan Audubon Society, and various other private citizens, uses a territory-mapping method to annually count Kirtland's warbler (*Dendroica kirtlandii*) singing males. Although the census procedure makes use of the behavior of male Kirtland's warblers to locate and count all the breeding males, it differs from the standard territory-mapping method in that only one pass through an area is made.

Spot mapping (Williams 1936) a variation of the territory-mapping technique. Ferris (1979) used the spot-mapping technique to examine the effects of Interstate 95 on populations of breeding birds in forest habitats in northern Maine. Numbers of breeding birds were determined on 12 study plots of 8 ha each, oriented at right angles to the highway. Each plot was censused along four 400-m transects, spaced 50 m apart. Transects were marked at 50-m intervals, providing a grid to aid location of singing males. Censuses were conducted during morning hours from late May through early July 1975-1977.

Best (1975) conducted a controlled study, with known territories and population size, using the territory-mapping procedure. Results from his investigation indicated that the method provides highly variable (and, at times, only very approximate) estimates of absolute numbers, at least for dense populations of species with small territories. Best also identified two major inherent errors in this census procedure: (1) observational bias, resulting from variability in the identification skill of observers, observation conditions (weather, time of day, etc.), screening effect of the habitat, and conspicuousness of the bird species; and (2) interpretational bias, resulting from differing interpretations of census data. Another major difficulty that Best highlighted was the absence of reliable controls to enable estimation of the magnitude and direction of error.

Territory-mapping is normally suitable only for counting the stationary part of noncolonial, passerine bird populations during the breeding season. This does not include "floaters"—those birds which are nonterritorial in behavior and often comprise a substantial but variable portion of the population. This shortcoming led Dawson (1981) to conclude that, for a minority of species, if surveyed at the right time, the territory-mapping method may yield a good density estimate. However, the method generally gives an index, not an estimate, of density. An index is a measure functionally related to density, that does not yield an estimate. See the INDEXES section in this report for more details.

Ground Counts

Ground counts include a number of population estimation techniques that do not fit neatly under the organizational headings offered in this report. Most of these techniques involve complete enumeration by direct counts without the use of remote sensing apparatus. Because of the myriad of estimation approaches included under this heading, generalized comments about the mechanics and assumptions underlying ground count methods are addressed, where possible, in the discussion of each technique.

Ground counts are appropriate for species which are conspicuous and relatively sedentary (Eltringham 1973). Some species satisfy these criteria but still are difficult to count accurately. Large populations in limited spaces, as reported by Eberhardt et al. (1979), may significantly limit accuracy. They also had trouble counting seals because of individuals hidden behind rocks and bushes or ice ridges and because of the various hazards of terrain and parents.

Eberhardt et al. (1979) suggested that ground counts could be used to develop correction factors for improving precision of aerial counts. These surveys are addressed in the "Remote Sensing" section of this report.

A major disadvantage of using ground techniques, however, is that they are somewhat disruptive because they generally require entering the colony.

Playback recordings show great potential for use in censusing highly vocal species of birds which are otherwise difficult to detect and count (Marion et al. 1981). Because vocalizations often stimulate a response by nearby individuals, tape-recorded calls may be used to locate birds (or other animals) and may improve the efficiency of the count. Braun et al. (1973) used tape-recorded male challenge calls to locate male white-tailed ptarmigan (*Lagopus leucurus*) in Colorado. Broody females were located by playback of recorded chick distress calls. Effectiveness of the techniques varied with weather conditions, time of day, and time of season. However, the use of tape-recorded calls more than doubled the number of birds observed per observer-hour and reduced time necessary for the census.

Wenger and Cringan (1978) placed radio instruments on six coyotes (*Canis latrans*) to evaluate a census technique involving siren-elicited howling in Colorado. These coyotes were located weekly by radio signal and were subjected to an automatic, electronic siren stimulus. Three coyotes readily howled in response to the stimulus and were heard at distances up to 1.6 km. The investigators concluded that, before using the siren technique, average response rates for an area would have to be determined to qualify the accuracy of the census results.

Many ground count surveys are erroneously purported to be complete counts. In addition, small differences between survey results at different times often are treated as meaningful. In these cases, testing is important, because it can demonstrate that small differences in or from the data can be attributed to sampling variation, and are not statistically significant. Agencies which conduct "complete counts" of wildlife should consider using an efficient sampling system instead.

Extermination

In some cases, a census can be made in conjunction with the extermination of a population. For example, an outbreak of hoof-and-mouth disease among the Jawbone mule deer herd, in California, in 1924, led to the first absolute tally of animals over a large area in the United States, using the extermination technique. Leopold et al. (1951) noted that strychnine-poisoned salt was first used. However, because the poisoned salt was not entirely effective on winter ranges, hunters were hired to kill the deer.

Another example of census by extermination is the use of fish toxicants. The normal function of fish toxicants in fisheries management is to destroy unwanted fish. Although approximately 40 chemicals have been used for the destruction of fish populations, only two (rotenone and antimycin) appear to have been used in fish censusing. The use of poisons is limited to areas in lakes or rivers where water is relatively shallow or slow-moving. Poisons are used in areas delineated by barrier nets placed across the channel of a river, across coves in a lake, or set out from a lake shore. In rivers, it is usually necessary to treat the water below the downstream net with potassium permanganate to destroy the toxicant and prevent any mortality outside the area.

The technique can give useful estimates of standing stock, presence of species, species composition, and strength of year classes (EIFAC 1975). The accuracy of the population estimate depends on the efficiency of collection of dead fish from the surface and bottom. In warm waters, kills are rapid, but accelerated decomposition of fish on the bottom may lead to an underestimate of the total number of fish killed. The cost of the technique may be low compared to other methods, although the use of a detoxifying agent increases the cost. Fry and juveniles are most difficult to collect, which may result in a serious underestimation of the population or biomass. The introduction of marked fish prior to poisoning may enable a correction to be made for fish not retrieved.

Platts et al.[2] report that explosion of primacord in small streams (up to stream order 4 or possibly 5) will kill almost all of the fish within 10 to 15 feet of the cord, provided that there are no major blocks between the explosive and the fish.

The stream area to be sampled should be blocked off with a net with mesh size small enough to keep young-of-the-year from leaving the area. Nets are needed to keep fish from moving out of the area while the grid is being laid, and to stop dead fish from floating downstream out of the sample area.

After each explosion, the dead fish are recovered by searching the stream channel. Most fish will be on the bottom. The streambanks must be inspected for occasional fish that are blown out of the channel. The net should not be pulled until the water clears, or at least until the water in the sampled area has had a chance to pass through the downstream net. The net should be inspected closely, because many fish will be caught in it.

Drive Counts

The drive count method evolved from the "deer drives" of pioneer days. This method uses counts of animals forced to leave a defined area by a traversing unit of "drivers" as the input for calculating population density estimates. The technique is usually modified for each particular area, but the procedures and features described by Overton (1971) provide a good general description.

(1) Two crews of observers are required. One drives the animal out of the area; the other, stationed around the perimeter of the area, monitors animals leaving or entering the area.

---

[2] *Platts, William S., Walter F. Megahan, and G. Wayne Minshall. 1981. Stream, riparian, and biotic evaluation methodology: Its design, use and value. Proposed for publication as a General Technical Report, USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah.*

(2) The area must have boundaries that can be monitored. Each monitor must be able to clearly observe the boundary at least as far as the next monitor.
(3) The monitors all look in the same direction around the boundary. Each monitor counts all deer leaving and entering the area between his post and the next monitor.
(4) Each monitor stops counting as soon as the drive crew has passed his station. This ensures that only one observer tallies each animal crossing the line.
(5) The drive crew lines up along one side of the area. The drivers then move through the area, keeping in line and in close spacing, driving the animals past the waiting monitors.
(6) The total number of animals is then calculated as the sum of the animals leaving the area ahead of the drive crew plus the animals passing back through the drive line, minus the animals entering the area ahead of the drive crew and the animals passing forward through the drive line.

If the drive area is surrounded by a suitable dirt road, the tracks of animals crossing the road can be counted instead of using monitors. The low efficiency of this technique makes it unlikely to be widely used.

Remote Sensing

Aerial Survey

Aerial survey is a practical means of estimating the number of large animals inhabiting an extensive area (Seber 1980). To refine this technique, investigators have used three approaches: (1) considering accuracy to be a sampling problem, with the success of a survey rated according to the size of the estimate's standard error; (2) detecting how far the mean of survey estimates is displaced from the true population size; and (3) treating aerial survey estimates as relative, rather than absolute, measures of abundance (Caughley 1974).

Populations are usually surveyed from the air by counting animals on a strip of known width, from an aircraft flying a straight line, at a constant altitude above the ground. This technique, the strip-transect method, one of three variations of line methods commonly used to estimate animal populations, also is discussed in that context later in this report. The field of search is defined for the observer by two marks or streamers on the wing strut. Between these, the observer scans a strip of ground which is of constant and known width when the aircraft is at survey altitude. Population density is estimated as the number of animals seen on the strip divided by the product of strip width and the length of the flight line (Caughley 1974).

Visibility bias may affect the results significantly. Caughley (1974) maintained that the height and speed of the aircraft and the width of the field of search affect the efficiency of the observer, causing negative bias in aerial censuses. As the width of the field of search increases, (1) the mean distance between an animal and the observer increases; (2) the time available to locate, recognize, and count an animal decreases; (3) the amount of eye movement needed to scan the strip increases; and (4) the mean number of obscuring items between the animal and the observer increases.

As cruising speed increases, the time available to locate and count an animal decreases, and the required rate of eye movement increases.

As altitude increases, the mean distance between the observer and the animal increases. Floyd et al. (1979) measured observability in an aerial census of deer in deciduous-coniferous habitat, in Minnesota. Testing the number of deer observed from the air against the known locations of radio-tagged deer, they found that approximately 50% of the deer were observed from the air.

Other influences on the efficiency of observers can be important sources of bias—in particular, boredom, fatigue, and time of day (Norton-Griffiths 1976). Boredom results in a decrease in awareness when an observer is searching a large unit without break. Fatigue develops as the census proceeds. Time-of-day has a number of effects. The increasing heat and turbulence around midday may lead to discomfort and air sickness. Erickson and Siniff (1963) found that air turbulence did not affect survey coverage, but may have affected the comfort and state of mind of the survey crews. The direction of incident light makes counting difficult early in the morning (Buechner et al. 1963) and late in the afternoon; towards midday the animals seek shade and become difficult to locate.

The construction and maneuverability of the aircraft used in aerial surveys, coupled with the experience of the pilot and observer(s), can significantly affect the precision of the estimates of the population being studied (Nichols 1980).

The Iowa Conservation Commission conducted an evaluation in 1979 of an aerial deer census technique over deciduous timber areas. Straight-line transects were flown over three study areas comprising 1,959 ha, using established landmarks and aerial photographs as reference. Outer limits of transects (200 m in 1978 and 400 m in 1979) were marked by a piece of tape on the airplane's wing strut.

Counts were made from a Piper Tri-Pacer[3] airplane flying at 130 kph. Two observers were seated in the back and counted deer in the transect on each side of the airplane. A strip about 50 m wide, directly below the airplane, was not visible to either observer; therefore, deer in this area could not be counted. Counts were made only after a fresh snow of 8-10 cm, so that vegetation patterns could not be mistaken for deer.

Survey results indicated that the aerial survey technique is less variable in areas with higher population densities of deer. Because survey flights took place over a 3-week period, many deer moved into and out of the study areas. Failing to count a deer on low deer density areas has a much greater effect on mean number seen

---

[3] *The use of trade and company names is for the benefit of the reader; such use does not constitute an official endorsement or approval of any service or product by the U.S. Department of Agriculture to the exclusion of others that may be suitable.*

than failing to count a deer on a high deer density area. Also, movement of deer into or out of a small survey area with a low density of deer would have a greater effect on survey results than would such movement in a high density area.

Results of this investigation also indicated that both bright, sunny days and dull, cloudy days should be avoided when conducting an aerial survey of deer. There should be enough light to allow good contrast between deer and their background, but not so much that shadows are heavy.

Kushlan (1979) censused colonially nesting wading birds with helicopters because of their slow speed and excellent visibility. He found that censusing from fixed-wing aircraft provided poor data for many species, particularly for colonies of birds nesting within the tree canopy. Buckley and Buckley (1976) noted, however, that helicopters are believed by some to disturb nesting birds substantially. Eberhardt et al. (1979) stated that rotor noise apparently causes many marine mammal species to either leave haulout areas or to dive.

Kushlan concluded that helicopter censuses should be used if the level of disturbance is acceptable, the increased accuracy is needed, and if the colony sites and species present are suitable.

Caughley (1974) stated that the strongest influence on the visibility of animals from the air is the time available for scanning the census strip. He concluded that visibility was inversely related to the speed of the aircraft. However, the effect of time limitation could be circumvented by photographing the strip and counting the animals in the laboratory.

Photography is a considerable aid to aerial survey, and is used extensively to census large groups in open country. It is less efficient than the unaided human eye when cover is available to the animals. An observer can view an animal from several angles while flying past it. The camera takes one look from one angle and misses any animal obscured at that moment (Caughley 1974).

Norton-Griffiths (1976) stated that undercounting bias can be minimized by photographing all groups of animals containing more than some specified minimum numbers. Norton-Griffiths warns, however, that a visual estimate of group size should be made and recorded at the same time in case the pictures do not turn out well. Eberhardt et al. (1979) emphatically state that counts of marine mammals should be made from photographs whenever possible if sizable numbers are involved.

Ultraviolet photography has been used (Lavigne and Oritsland 1974, Lavigne et al. 1975) to distinguish white-coated animals (harp seals (*Phoca groenlandica*) and polar bears (*Ursus maritimus*)) on backgrounds of snow and ice.

Eberhardt et al. (1979) discussed two techniques for obtaining correction factors to improve the precision of population estimates. One is to derive equations separately and then arbitrarily apply them in a census at a different time and locale. However, the correction factors may not remain constant over time and space. The second approach is to utilize part of the resources of the main survey to obtain the correction factors and to do so as an integral part of the survey. In such a scheme, counts would be taken on a single area throughout the time that the main survey counts are made. The auxiliary counts should be spread throughout the time interval covered by the main survey and conducted in an area with enough animals present to reduce the effects of chance fluctuations of individual behavior.

One method for deriving correction equations as part of the main study is to conduct simultaneous aerial and ground counts of the same restricted areas. One of the most extensive applications of such a "ground truth" method is the waterfowl breeding ground counts cooperatively conducted by the U.S. Fish and Wildlife Service, the Canadian Wildlife Service, and various state and provincial wildlife agencies. Each year, more than 3.37 million km^2 of breeding habitat in Canada and the United States are sampled systematically to estimate the breeding population of 20 species of ducks.

Martin et al. (1979) describe the sampling scheme as a modification of a double sampling plan with stratification. A systematic sample of units is selected, with the first transect located randomly in each stratum. These transects are flown in fixed-wing aircraft at a height of 30.5-45.7 m above the ground; and all observed, identified waterfowl are counted for 1/8 mile (201 m) on each side of the aircraft. The number of birds is then counted on the ground within units comprising a subsample of the units in the aerial sample. The relationship between the air and ground counts for the subsample is used to adjust the much larger sample of air counts to a ground-count basis, accounting for birds on the ground that are not seen from the air.

The efficiency of this design depends on the relative cost of taking the two measurements, the strength of the relationship between the two procedures, and the variability of the estimates from each sample within a stratum. Martin et al. (1979) present examples of general applications of the design, including estimation of the population size for a particular species in a stratum.

Thermal Infrared Scanners

The potential for detecting and censusing big game by remote sensing of thermal infrared radiation emitted by the animals has long been recognized (Croon et al. 1968). Airborne, thermal infrared scanners have been used to detect white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), and moose (*Alces alces*) (Reeves 1975). The technique is applicable to censusing open-range animals such as caribou (*Rangifer tarandus*), bison (*Bison bison*), pronghorn (*Antilocapra americana*), etc. (Croon et al. 1968).

Imaging infrared sensors are line-scanning devices which produce images closely resembling photographs. When mounted in an aircraft with the scanning direction perpendicular to the direction of flight, the forward motion of the aircraft and the scanning action of the optical system permit a large area of terrain to be scanned in a short time. As the field of view moves, a detecting device scans terrain objects of differing emittance or reflectance characteristics and relays signals to the signal processing and display system. This system amplifies the relatively weak signals from the detector and then uses the amplified signals to produce a visible image (Croon et al. 1968).

Line-scanning systems provide a continuous recording of the spatial variation in average energy received from the total area within their instantaneous field-of-view. To be detected as different from its background, an animal must emit enough energy to produce an instantaneous response, averaged over the entire field-of-view, which is greater (or smaller) than the response produced by the background alone. This difference must be large enough to permit the signal processing system to discriminate between signals with animals and signals with no animals (Croon et al. 1968). The actual surface temperature of a deer at a particular time depends on a number of environmental factors: (1) air temperature, (2) solar radiation, (3) atmospheric water vapor pressure, and (4) wind speed (Parker and Driscoll 1972).

Consideration of thermal contrast between animals and other background components is an important factor in a general evaluation of this technique. Studies of deer detectability have been conducted almost exclusively in winter because of the high probability of snow backgrounds and the considerably reduced size of the geographic area which must be covered. Most modern scanners can detect deer from an altitude of 500 to 1,000 feet against a complete snow background (Reeves 1975).

Because the technique involves heat instead of visible light, scanning can be done at night, when animal activity is frequently greatest (Croon et al. 1968). Although overall thermal contrast is reduced during this period, it still may be sufficient for detection. However, as a practical matter, flying at low altitude in the dark is hazardous over much of the deer winter range because of rough topography (Reeves 1975).

The primary limitation of this technique is the inability of the radiation to penetrate vegetation. This precludes the use of thermal scanning for deer detection, in summer, in most areas of the U.S., because the animals tend to be on ranges with a tree overstory. Where the overstory consists of deciduous species, animals can best be detected after the leaves fall. Seasonal and diurnal habits of the animals may be used to advantage (i.e., movement of mule deer onto winter range areas; occupation of open yarding areas by white-tailed deer in the Northeast) (Reeves 1975).

Difficulties of distinguishing between animals of similar size is a major problem (Croon et al. 1968). Parker and Driscoll (1972) reported that interpreters made many errors when attempting to separate mule deer and pronghorn. The criterion for separating the species was the shading of the spots on the image. Because their temperature is higher and their size is larger, deer produced a lighter image than the pronghorn. Croon et al. (1968) suggests that a total count of mixed species may be useful, provided that the relative number of each species can be determined from ground samples. Graves et al. (1972) warn that false target detection is a problem to the untrained interpreter. The infrared signal from large rocks sometimes appear warm in their study images at about the same intensity as the infrared signal from deer.

Flight altitudes must be considered as they relate to the size of the target to be detected. Parker and Driscoll (1972) failed to detect mule deer from an altitude of above 500 feet, whereas Graves et al. (1972) easily detected individual livestock during the summer, at 1,000 feet altitude. The highest altitude that permits good detectability should be used, to maximize the area covered during each pass (Graves et al. 1972).

Wride and Baker (1977) listed the disadvantages of the technique for census of ungulates as (1) restricted use in severe terrain and southern latitudes, (2) inability to determine sex of animal, and (3) inability to separate species except when they are different sized animals. They found the cost is comparable to helicopter census work.

Thermal infrared scanning requires specialized expertise and sophisticated equipment. As with conventional aerial photographs, training and experience are necessary for proficiency in interpreting infrared imagery. The selection of a specific infrared detector depends primarily upon the general environmental conditions expected during the time of the survey and the specific type of target to be detected.

Currently, it is not possible to actually "see" small mammals with existing remote sensors (Reeves 1975). However, evidence of their presence by den construction activities and changes in the intensities of these activities also can be used to evaluate population dynamics (Reid et al. 1966).

Acoustic Methods

Acoustic methods for detecting fish were introduced in the 1930's and have been used consistently since then for estimating the abundance of fish. The method depends largely on interpretation of the signals from a calibrated echo-sounder.

Methods for processing signals include visual inspection and measurements from standard echograms, electronic integration of signals corrected for losses associated with different fish depths, and computer analysis of signals as recorded on magnetic tape. Computer analysis permits separate estimates for various depth strata and for several levels of amplitude.

If the population is sparse, echo counting based on "point" signals can be used. For high density populations, such as schools, a cumulative method using an echo integrator is more approprate. If other sampling methods, such as netting, are used for calibrating the counts, then the estimates can be converted to absolute estimates of abundance (Seber 1981).

Winn et al. (1975) used a combination of acoustic methods and visual tracking to estimate the population of the humpback whale (*Megaptera novaeangliae*) in the West Indies. Population estimates were lower by the acoustic method, because only single adults call. Also, when a large group is calling simultaneously, it is difficult to distinguish individual calls. This is a distinct disadvantage of the acoustic method, in addition to the great expense of purchasing and installing the equipment. However, there are several advantages to the acoustic method—it can be used day and night, continuously or intermittently, in between other ship programs, and while other sampling is occurring.

Acoustic gear has been used successfully in deep freshwaters, but in shallow waters of both lakes and rivers, the methodology is less well defined. Identification or separation of species by acoustic means is not yet feasible (EIFAC 1975).

In addition to sampling errors, Seber (1981) outlines several operational and behavioral problems inherent with acoustic methods.

The FAO (EIFAC 1975) expects that the high cost of acoustic survey equipment will be reduced with advances in miniaturization, better knowledge of sampling requirements for given levels of precision, and the use of shore-based instead of on-board computers.

Temporal Census

As noted before, a temporal census is one in which a count is made of all animals passing a specific place during some interval in time. Temporal census techniques are suitable in the following situations (Overton 1971):

(1) anadromous fish passing through fish ladders on dams,
(2) birds entering roost sites, and
(3) migrating animals using a well-defined route.

Fish traps are the simplest installations for counting and identifying migratory fish passing through fish ladders, because all fish moving upstream must go through the ladder. Automatic fish counters can be installed easily in fish ladders. Fish may be counted electronically, acoustically, magnetically, electromechanically, or optically. Installation of a series of automatic fish counters along river or stream systems is recommended to increase accuracy (EIFAC 1975).

Where site conditions permit, a fish barrier can be built across the full width of a river, allowing a complete count of the upstream and downstream migration. Otherwise, it still is possible to sample a portion of the run. Because of the cost involved, the use of devices employing fish fences extending across the full width of the river channel is restricted to smaller river systems and the tributaries of large rivers.

The roosting phenomena of certain birds can provide opportunities for using temporal census techniques, but the resulting estimates, at times, have proved quite controversial. Using counts of wood ducks (*Aix sponsa*) conducted during the autumn roosting flights as a population index, Hein (1965) and Hein and Haugen (1966) concluded that fall roosting flight counts could furnish an index which would detect changes of 15% in annual abundance of wood ducks. In contrast, Tabberer et al. (1971) concluded that flight counts in Louisiana were invalid because of variations in quality and stability of individual roosts. Smith (1958) felt that the technique in Louisiana was invalid because of yearly fluctuations in the amount of surface water in roosts.

Parr and Scott (1978) state that if a roost count is to be a valid index technique, the following assumptions must be met: (1) each roost must be a geographically discrete area containing an identifiable wood duck population separate from other roosts; (2) the number of wood ducks using a roost must reflect the general abundance of the species in the area, and the wood ducks must congregate at the roost solely as a result of their social needs, not because of the presence or absence of food or water elsewhere; (3) all, or at least a consistent proportion, of the wood ducks flying to a roost must be susceptible to being counted during any given counting event; (4) all, or at least a consistent proportion, of the wood ducks in an area must fly to identifiable communal roosts in the evening; and (5) there must be little unilateral interroost movement.

The temporal census approach can be used to estimate populations of animals which move or migrate seasonally. Extensive migrations of the gray whale (*Eschrichtius robustus*) between summer habitat off Alaska and the breeding lagoons near Baja, California, provide some unique opportunities for censusing. The migration route passes very close to the California coast, so that it is possible to attempt to count the entire population. A similar effort has been started for the northward migration of bowhead whales (*Balaena mysticetus*) into the Arctic (Eberhardt et al. 1979).

CLASSICAL SAMPLING METHODS

Estimation of population size by sampling techniques has several principal advantages over methods involving complete enumeration (Cochran 1977):

(1) Reduced cost.
(2) Greater speed. The data can be collected and summarized more quickly.
(3) Greater scope. Surveys which rely on sampling have more scope and flexibility as to the types of information that can be obtained. Limitations on availability of trained personnel or specialized equipment may render a complete census as impractical.
(4) Greater accuracy. Because only a portion of the total area or population is measured, greater care can be exercised in the measurements; supervision can be improved; fewer, but better trained personnel can be used; and the probable number of nonsampling errors can be reduced (Husch et al. 1972).

In wildlife studies, a two-stage process is often used in the survey design. The first stage is selecting sampling units that are representative of the overall study region in both space and time. The second stage consists of taking a sample on each unit in order to estimate the parameter(s) of main interest, usually abundance. Specialized methods, such as capture-recapture, removal, line transects, etc. are used only at the second stage (Eberhardt 1978a). The complete enumerative methods outlined earlier also can be applied at the second stage to determine the abundance of selected subpopulations contained within the sampling units.

Sampling Unit and Sample Size

The determination of the optimum type of unit is important in the economics of sampling. A change in the type of unit usually affects both the cost of taking the sample and the precision obtained from it. The optimum unit is that which gives the desired precision for the sample estimates at the smallest cost, or the greatest precision for fixed cost (Cochran 1977).

Types of units should always be compared in terms of the kind of sampling that is to be used within the units, or, if this has not been decided, for the kinds that are under consideration. Changes in the method of sampling within units will change the relative net precisions of the different types of units. Unless one type of unit is uniformly superior, some compromise decision is made, giving principal weight to the most important criteria. Because it is seldom feasible to make a survey solely for the purpose of comparing different types of units, information about optimum type of units is usually a byproduct of other surveys (Cochran 1977).

The decision about the size of the sample is important. Too large a sample implies a waste of resources; too small a sample diminishes the utility of the results. Cochran (1977) gives formulas to use in determining sampling intensity.

Simple Random Sampling

Simple random sampling is the fundamental selection method. Other sampling procedures are really modifications intended to achieve greater economy or precision (Husch et al. 1972).

Simple random sampling is a method of selecting a number of sampling units out of the population so that every one of the possible sampling units has an equal chance of being chosen. In practice, a simple random sample is drawn unit by unit. The units in the population are numbered from 1 to *N*. A series of random numbers between 1 and *N* is then drawn, and the units which bear these numbers constitute the sample. At any stage in the draw, this process gives an equal chance of selection to all numbers not previously drawn (Cochran 1977).

When a unit has been selected, it is not replaced, because this might allow the same unit to enter the sample more than once.

Cochran (1977) summarized the analysis procedures for the resulting data from the sampling units.

Stratified Random Sampling

In stratified sampling, the population is first divided into subpopulations. The purpose of stratification is to reduce the variation within the subdivision and to increase the precision of the population estimate (Husch et al. 1972). The subpopulations are nonoverlapping and together make up the whole of the population.

The subpopulations are called strata. When the strata have been determined, a sample is drawn from each stratum, the drawings being made independently in different strata. If a simple random sample is taken in each stratum, the whole procedure is described as stratified random sampling.

Stratification is a commonly used technique for the following reasons (Cochran 1977):

(1) If data of known precision are wanted for certain subdivisions of the population, it is advisable to treat each subdivision as a "population" in its own right. (Husch et al. 1972.)
(2) Administrative convenience may dictate the use of stratification (e.g., the agency conducting the survey may have field offices, each of which can supervise the survey for a part of the population).
(3) Sampling problems may differ markedly in different parts of the population.
(4) Stratification may increase precision in the estimation of characteristics of the whole population. The basic idea is that it may be possible to divide a heterogeneous population into subpopulations, each of which is internally homogeneous. If each stratum is homogeneous, in that the measurements vary little from one unit to another, a precise estimate of any stratum mean can be obtained from a small sample in that stratum. These estimates can then be combined into a precise estimate for the whole population. (Husch et al. 1972.)

Husch et al. (1972) cited the disadvantages of stratification:

(1) The size of each stratum must be known, or at least a reasonable estimate must be available.
(2) Sampling units must be taken in each stratum, if an estimate for that stratum is needed.

Strata can be selected on the basis of criteria such as topographic features, habitat types, etc. An arbitrary form of stratification is often used in sampling large areas where there is little basis for some kind of natural subdivision. In this case, the area can be broken into uniform-sized squares or rectangles, even though the resulting blocks may not contain homogeneous subpopulations. Still, it is reasonable to assume greater homogeneity within a smaller block than in the larger, entire area (Husch et al. 1972).

The different strata into which an area may be divided can be irregular in shape, of varying sizes, and of different importance. Stratification permits the sampling intensity and precision to be varied for the several strata. To estimate the number of sampling units needed, it is necessary to have preliminary information on the variability of the strata in the population, and to choose an allowable error and probability level similar to the technique used for simple random sampling. With this information, the intensity of sampling can be estimated. The total number of sampling units can then be allocated to the different strata either by proportional or optimum allocation.

Cochran (1977) discusses the analysis procedures for data obtained from stratified random sampling.

Systematic Sampling

In systematic sampling, the sampling units are spaced at fixed intervals throughout the population but with some type of random starting point. Inventories using a systematic sampling design have advantages: (1) they provide good estimates of population means and totals by spreading the sample over the entire population; (2) they are usually faster and cheaper to execute than designs based on probability sampling, because the choice of sampling units is mechanical and uniform, eliminating the need for a random selection process; (3) travel between successive sampling units is easier because fixed directional bearings are followed, and the resulting travel time consumed is usually less than that required for locating randomly selected units; and (4) the size of the population need not be known, because every unit at a fixed interval is chosen after an initial random starting point has been selected. The sampling then continues until no further sampling units are found (Husch et al. 1972).

The primary disadvantage to systematic sampling is the lack of available methods for estimating sampling error.

The larger the area inventoried, the greater the amount of variation that can be expected and the more likelihood that a systematic sample will give a more precise estimate than a completely random or stratified random sample. The precision of a systematic sample estimate is better than that of a simple random estimate when the systematic sample contains more variation than is likely in the population (Cochran 1977).

Multistage Sampling

Multistage sampling is basically a means of working down to a sampling unit of manageable size (Lewis 1970). In multistage sampling, a population consists of a list of sampling units (primary stage), each of which is made up of smaller units (second stage), which, in turn, could be made up of still smaller units (third stage). A random sample would be chosen from the primary units. A random subsample of the secondary units would then be taken in each of the selected primary units, and the procedure would be continued to the desired stage. This procedure is called multistage sampling in general. Two-stage sampling, the most common application, indicates the sampling stops at the secondary stage. For example, an area to be inventoried might consist of numerous compartments that could be considered the primary units in a sampling design. Plots chosen in the selected compartments would then form the secondary units (Husch et al. 1972).

Multiphase Sampling

The most used adaptation of multiphase sampling involves two phases and is often referred to as double sampling. In double sampling, an estimate of one variable is obtained by utilizing its relationship to another. The method is of most interest when information on the principal variable is costly and difficult to obtain, and the secondary and related variable can be more easily and cheaply observed. Thus, the aim of double sampling is to reduce the number of measurements of the costly variable without sacrificing precision of the estimate.

The general procedure in double sampling is that in a first phase a large random sample is taken of a secondary or auxiliary variable, X, which will yield a precise estimate of its population mean or total. In a second phase, a random subsample is taken from the previous sample, and on these sampling units, measurements are taken of the principal variable, Y. Note that the first and second phases are mutually dependent, because the measurements in the secondary phase are taken from a portion of the sampling units of the first phase. The result is a small sample on which both the auxiliary and principal variables, X and Y, have been measured. With these data, a regression can be developed between the two variables which can be utilized with the large sample of the auxiliary variable to make an estimate of the mean and total for the principal variable (Husch et al. 1972).

LINE METHODS

Line methods may be listed in three general categories: (1) line-intercept method, (2) strip-transect method, and (3) line-transect method.

The line-intercept method has been used by plant ecologists for many years. The method depends on the interception of an object by a line. Eberhardt (1978b), prompted by McIntyre's (1953) work on estimating plant densities, investigated the use of this method to estimate the number of den sites in a large, prairie dog (*Cynomys spp.*) town, in North Dakota. He suggested that the line-intercept method is appropriate in situations where detection depends mainly on the observer, such as with animals that do not respond to the observer's presence or with inanimate objects.

In the strip-transect method (also called the belt-transect method), counting is restricted to a strip of prescribed width. The simplest case of a strip transect is when the objects being sampled are readily visible and sufficiently abundant to permit using a restriction on width of the strip covered (Eberhardt 1978b). This method is widely applied during aerial surveys and was discussed earlier in that section.

Line-transect sampling has been used to obtain estimates of animal abundance since at least the early 1930's. The use of line transects may be considered a plotless method (Burnham et al. 1980). The observer traverses a sampling unit on a randomly selected straight line. Essentially, the same design consideration of line placement is needed in line-intercept, strip-transect, and line-transect sampling. Two distances may be recorded—one the direct distance to the object when it is first seen (the radial distance), and the other the distance from the transect to a line drawn through the object parallel to the transect (the right-angle distance) (Eberhardt 1978b). The sighting angle also can be recorded (Burnham et al. 1980).

Estimation of density can be based either on perpendicular distance or on sighting distances and angles. If sighting distances and angles are taken, the perpendicular distance can be computed after the data are collected. Valid estimation is not possible based solely on sighting distances; however, valid inferences can be based solely on perpendicular distances (Burnham et al. 1980).

Four assumptions are critical to obtaining reliable estimates of population abundance from line-transect sampling (Burnham et al. 1980):

1. Points directly on the line are never missed.
2. Points are fixed at the initial sighting position; they do not move before being detected, and none are counted twice. Movement is not critical if it is independent of the observer and "slow" relative to the observer's speed along the line.
3. Distances and angles are measured exactly, with no measurement errors or rounding errors.
4. Sightings are independent events. The flushing of one animal does not cause another to flush.

Basically, any convenient method of locomotion that will not violate these four fundamental assumptions can be used.

Mikol (1980) stressed the importance of understanding both the advantages and disadvantages of transect sampling when selecting a method to estimate bird population densities for a particular study. Some advantages are:

1. Transects can be used at any time of the year, and results for different seasons or months can be compared.
2. Each run of a transect on each transect line can be considered a sample replicate. In addition, if the line transect estimators discussed by Gates (1979) and Burnham et al. (1980) are used, sampling variances for the density estimates can be calculated.
3. Strip-transect and line-transect sampling are generally less time consuming and easier than other methods of collecting data for population density estimates (Emlen 1971).

Disadvantages of transect methods include the following:

1. The observer must be able to estimate all distances correctly (at least by distance intervals) for line transects or the data will not meet the requirements for data analysis.
2. It is difficult to determine the correct width of the belt in strip-transect sampling. A wide belt may result in incomplete sampling for some species, if there is a decrease in species detectability with distance. A narrow belt may also miss some species, especially those with large home ranges (Mikol et al. 1979). A narrow belt also has a very large edge relative to its area, which may result in a high variability of population estimates because of animals moving into and out of the belt.
3. The distribution of right-angle distances with line transects or, equivalently, the effective width, often will be different for different species.
4. An inaccurate estimate of population density may be obtained if the frequency histogram of right-angle distances for the data collected does not fit the distribution pattern required for the sampling method used (Gates et al. 1968). Some of the more recently developed data analysis methods do not require the data fit any particular distribution in order to obtain reliable results from line-transect sampling (Burnham et al. 1980).

Burnham et al. (1980) discuss the development of line-transect sampling and show a basis for the general construction of line-transect estimators. They developed the following line-transect density estimator:

$$\hat{D} = \frac{n\hat{f}(0)}{2L} \qquad [1]$$

where the units of $\hat{f}(0)$ are the reciprocal of the units of the perpendicular distance x, $L =$ line length, and $n =$ number of animals seen.

Mikol (1980) provides guidelines for conducting transect studies for nongame birds to include aspects of study design, observer training, setting up transects, preparing field forms and maps, field sampling, and recording data.

The selection of a sample size requires advance information on the variability of $\hat{D}$ as a function of the line length. Burnham et al. (1980) provide a discussion of the equations needed and provide an example for determining sample size when using line-transect sampling.

Numerous factors affect the probability of detecting objects, including weather conditions; the alertness, interests, and training of observers; habitat conditions; time of year; time of day; group size (for clustered populations); species; sex; and age. The problem most frequently encountered in applying line transects to wildlife populations is that animals move to avoid the observer. Such behavior tends either to increase the perpendicular distance of the animal from the line or cause the animal to be missed (see assumption number 2). Movement is less of a problem during aerial transect sampling. However, the inability to see all animals on the line becomes a problem with aerial transects (Burnham et al. 1980).

Two computer programs provide various estimators of density using the line-transect data: TRANSECT, developed by Laake et al. (1979), in conjunction with Burnham et al. (1980); and LINETRAN, developed by

Gates (1979). The availability, procurement, and documentation of program TRANSECT are discussed by Burnham et al. (1980). LINETRAN is a FORTRAN computer program that computes a variety of estimators (12) for the line-transect method of sampling biological populations. The characteristics of this program are discussed by Gates (1980).

The degree to which mobile populations can be surveyed by line-transect methods depends on the degree to which the inherent assumptions can be closely approximated. If the subject of the study is a highly mobile animal, serious problems caused by movement can arise, often to the extent of rendering line-transect sampling useless for such species. Populations which are routinely submerged underwater or are burrowed underground and those which assemble in loose groups and run, rather than flush, are not appropriate for line-transect methods (Burnham et al. 1980).

POINT METHODS

Ramsey and Scott (1979) presented an adaptation of line-transect methodology to circular-plot surveys. This technique was developed for surveying bird populations in rough terrain. The procedure consists of crossing the target region with a series of transects, along which stations are marked at regular intervals. An observer arrives on station, waits until the effects of his arrival have subsided, then begins a count which lasts a fixed amount of time.

For each bird detected at a station, its distance from the station is recorded. These distances are used to estimate the area which is effectively surveyed. This feature allows estimates of species density to be made.

The region surveyed around a station is viewed as a circular plot; however, all detections are recorded, so that the procedure is "plotless," like a line transect. As with line-transect methods, the total number of detections, divided by an estimate of the area surveyed, is the estimate of population density. The area surveyed acquires a very precise definition in terms of an effective radius of observation, which, in turn, is a well-defined parameter in the statistical model, summarizing an observer's inability to detect distant objects.

Ramsey and Scott (1979) identify several assumptions about the design parameters of this variable circular-plot survey technique:

1. The plot radius is large enough that all detection distances are below it.
2. Both the distance between transects and the distance between stations along a transect exceed twice the plot radius, so that no object is detectable at more than one station.
3. The pause time between arrival on station and count period is long enough to ensure that there is no effect of observer presence on the location or detectability of objects in the plot.
4. The length of count period is long enough to ensure that all objects within the immediate vicinity of the station are detected.
5. The count period is short enough to warrant the assumption that objects occupy fixed locations during the count.
6. No object is counted more than once at a given station.
7. The time between arrivals of observers is adequate to eliminate observer effects as in (3).

Szaro and Jakle[4] assessed the applicability of the variable circular-plot method to riparian and desert scrub habitats and compared the results of using this method with those gained from the territory-mapping method. They concluded that the territory-mapping method is time consuming and requires more effort to census common bird species than the variable circular-plot method. Many of the rarer species, however, were not adequately censused by the variable circular-plot method. They stated that the advantages of the variable circular-plot method are that it (1) is not limited to the breeding season, (2) is usable in small habitat "islands," and (3) yields population density figures with an estimate of precision.

SPATIAL DISTRIBUTION METHODS

Several techniques have been developed which use the distances of individuals from randomly chosen points (closest-individual techniques) or the distances between neighbors (nearest-neighbor techniques) to calculate estimates of population density (Seber 1973). The background theory for these techniques is provided by Kendall and Moran (1963).

Distance methods can be used for animals which are relatively immobile and readily seen, or for well-marked colonies (Seber 1981).

Seber (1973) found that, because of sampling difficulties, and the present lack of supporting statistical theory, the closest-individual techniques are preferable to the nearest-neighbor techniques for estimating population density.

Distance estimators of density, which assume a randomly distributed population, may exhibit serious bias unless the population under consideration forms a completely random spatial pattern (Diggle 1975). This requirement severely constrains the usefulness of these methods (Andrewartha and Birch 1954).

Batcheler and Bell (1970) presented a method which utilizes both types of measurement for estimating the density of a random or of a nonrandom population. It employs the distance from each sample point to the nearest population neighbor, from that individual to the nearest neighbor, and from that neighbor to its nearest neighbor. The principle of the model is that an estimate of density is first obtained based on the distances from the sample point to the nearest population member. This point-distance estimate is then corrected for bias arising from nonrandomness by using the sums and frequencies of first and second neighbor distances.

---

[4] *Szaro, Robert C., and Martin D. Jakle. 1981. Comparison of variable circular-plot and spot-map methods for estimating avian densities in desert riparian and scrub habitats. Poster paper presented at an International Symposium on estimating numbers of terrestrial birds held at Asilomar, Calif., October 26-31, 1980.*

Diggle (1979) provided a review of the spatial point processes which have been suggested as possible models for point patterns in ecology. Because many of the methods are relatively new and untried, Diggle feels that firm conclusions cannot yet be drawn on the relative merits of the various methods.

INDEXES

Many management surveys provide only indexes to population levels. Eberhardt (1978a) defines an index as a measure that does not directly yield an estimated density (number per unit area) but that is functionally related to density.

The various indexes can be described as two distinct types (Overton 1971):

1. A count of animals, calls, or signs made in a manner which does not allow direct population estimate by application of sampling theory. This is a sample census without known sampling probabilities (e.g., roadside counts).
2. An estimate of the number of animals based on counts of some associated population. The method yields at one extreme a virtual tally of a population (i.e., track counts of quail in snow) and, at the other, indexes which are very difficult to calibrate (e.g., call-counts).

Indexes for estimating relative density are particularly useful in detecting changes over time or in comparing populations in different areas. However, if any comparisons are to be made, the surveys should be carried out under as nearly identical conditions as possible. Because changing conditions have different effects on different indexes of density, using more than one type of index is desirable (Seber 1981).

Where possible, replicated samples should be used for determining indexes, so that sampling estimates of variance can be calculated. Seber (1981) provides an example using roadside counts.

An index can be "calibrated" to account for the recognized effect of external variables such as weather or time of day (Overton 1971). Attempts to calibrate an index against some direct estimate of population abundance could be considerably complicated if the underlying relationship is not linear. Another complication is the bias introduced by sampling (chance) errors in both variables. In such a situation, ordinary regression analysis will yield a biased estimate of the slope, and therefore, result in a biased calibration equation (Eberhardt 1978a).

Eberhardt (1978a) stated that the coefficient of variation of many kinds of index data seems sufficiently constant in practice to supply an approximate guide for planning purposes. For any particular locale for which an index is to be developed, prior data offer the best source for a variability estimate to be used in planning. When such data are not available, or when a choice of methods is under consideration, Eberhardt (1978a) provided a useful table of population coefficients of variation that might be expected from various species. This table can be used for determining sample sizes to achieve a desired level of precision in the estimation.

The Auditory Index

Generally, the index of auditory signals of animal presence is constructed from data gathered by observers passing through an area, using standardized procedures concerning selection of route, starting and stopping time, number of stations per route and season of the year. Auditory activity, like other animal activity, is influenced by time of day, weather conditions, season of the year, mating status, and many other factors. Some procedures are attempts to adjust indexes for effect of such factors. The technique of multiple regression is well suited to simultaneous considerations of indexes and external factors of interest for predictive purposes.

The index developed from the mourning dove (*Zenaida macroura*) call-count survey is used as a guide in setting hunting regulations (Blankenship et al. 1971). More than 1,000 routes throughout the United States are surveyed annually between May 20-June 10. Each call-count route consists of twenty, 3-minute listening points at 1-mile intervals along roads. Records are kept of the number of doves heard calling, number of calls, and number of doves seen along each route. Analysis is based on doves heard.

Blankenship et al. (1971) demonstrated that stratification of these routes, based on Küchler's map of potential vegetation, resulted in a significant reduction in the error variance when compared with physiographic stratification (Fenneman 1931, 1938). They concluded, on the basis of statistical considerations, that the routes should be randomly selected within ecological strata, with the number of routes in each stratum presumably being inversely proportional to the variance (Gates et al. 1975).

Several studies have been designed to determine if call-count surveys could be utilized as indexes for breeding activity, eventual productivity, and fall population levels. Brown and Smith's (1976) analysis showed that call-counts probably were a valid survey technique for measuring population levels of white-winged (*Zenaida asiatica*) and mourning doves, and that the mourning dove call-count index could be used with reasonable accuracy to forecast early fall hunting success in Arizona.

Regression techniques can be useful for converting a relative index to an absolute density. Brown et al. (1978) showed that there is a potential to predict fall population levels of scaled quail (*Callipepla squamata*) from call-count surveys, as indicated by a significant linear relationship between the number of calling male scaled quail and hunting success.

Pellet Counts

Pellet-group counting is the process of estimating by fecal pellet-group counts, the actual or relative numbers of big game, or their days of use, in a given area (Neff 1968).

Plots are located in such a manner that the study area is adequately represented. Any of the sampling designs might be used. Then the number of pellet groups is counted in each plot and expressed in terms of pellet groups per unit of area. This expression is then divided by an assumed defecation rate to yield animal days utilization per acre for the study period. If the population is assumed to be constant, division of the latter index by number of days in the period yields the number of animals per acre (Overton 1971).

The chief advantage of this method is that pellet groups can be sampled by standard field plot techniques. Most pellet-group plots have been circles or long narrow rectangles, usually distributed in some form of stratified-random design. Sample plot layout often can be planned to minimize variance between plots or groups of plots (Neff 1968).

Pellet-group sampling is more efficient in areas of high pellet-group density. Winter ranges or other areas of concentration should be chosen for herd census or trend studies whenever possible (Neff 1968).

Daily defecation rates are needed for computing animal-days use or total numbers. Neff (1968) provides a summary of determinations of defecation rates for deer and other ruminants. High defecation rates in deer have been observed to accompany high feed intake, high forage moisture content, high percentage of young in the herd, change in diet from roughage to concentrates, and the impact of captivity (Neff 1968).

Observed differences in pellet deposition rates between male and female adult moose necessitate knowledge of the sex structure of a population when the pellet group census technique is utilized. This variation between the sexes complicates the technique and may preclude its use for moose in many instances (Franzmann et al. 1976).

Observer bias arises mainly from differences in interpretation and from missed groups. Because of missed groups, most counts underestimate actual pellet-group density. Missed groups error is influenced by plot size and shape, type and density of understory vegetation, and observer fatigue and inherent visual acuity. Sources of interpretational differences include decisions concerning peripheral groups, scattered groups, and the minimum number of pellets to be counted as a group. Common practice requires use of permanently marked plots which are periodically cleared. Temporary plots sometimes are used where the deposition period can be dated by reference to leaf-fall, by deformation of pellets caused by emergence of succulent feed, or by estimation of the period of herd occupancy of seasonal range. Such dating schemes introduce an additional source of observer bias (Neff 1968).

Pellet-group counts have been unworkable at times because of rapid loss of pellets through insect attacks or heavy rains, because of difficulties in identifying pellets of different species, or because of extremely dense vegetation.

In a few cases, the pellet-group count has been tested against known numbers of deer in fenced areas, or against other census techniques. The estimates have been reasonably accurate in many cases (Neff 1968).

Track Counts

Track counts of species have been used extensively as indexes, but the development of an estimator of populations requires specific modeling of the relationship between number of animals and the spatial distribution and abundance of tracks.

McCaffery (1976) investigated the use of deer trail counts in Wisconsin as a population index and a means for evaluating fall deer habitats. Deer trails (defined as distinct paths in ground vegetation and forest litter caused by repeated use by deer) were counted along transects in spring, before greenup, and in late fall, before snow accumulation. Results of trail surveys correlated well with numbers of bucks harvested per square kilometer. When the variation in hunting exploitation between units is considered, agreement of these two indexes is remarkably close. A highly significant coefficient of correlation was produced when trail counts were compared with results of spring pellet-group surveys for those units where pellet counts were conducted within 1 year of the trail survey.

Linhart and Knowlton (1975) investigated the method of determining the relative abundance of coyotes (*Canis latrans*) using artificial scent stations in 17 western states. Each scent station line consisted of 50 scent stations, at 0.3-mile intervals, along a contiguous, 14.7-mile route. Each station was a perforated-plastic capsule containing a fermented-egg attractant placed in the center of a 1-yard circle of sifted dirt. Animal visits (based on tracks) were recorded for each station daily, for 5 consecutive days, during September, to provide an index to compare coyote population trends.

The data from each survey line were tabulated by subtracting the number of instances when scent stations were inoperative from the total of 250 station-nights (50 stations × 5 nights) to give the total number of "operative station-nights." The total number of visits recorded for each species during the 5 nights was then used to calculate an index of relative abundance as follows:

$$\frac{\text{Total animal visits}}{\text{Total operative station-nights}} \times 1{,}000 = \text{index} \quad [2]$$

In addition to coyotes, the surveys have recorded the presence of domestic dogs, red wolves (*Canis rufus*), red fox (*Vulpes vulpes*), kit fox (*Vulpes macrotis*), swift fox (*V. velox*), gray fox (*Urocyon cinereoargenteus*), and a variety of noncanid carnivores—black bears (*Ursus americanus*), raccoons (*Procyon lotor*), ringtails (*Bassariscus astutus*), weasels (*Mustela* sp.), mink (*M.*

vison), skunks (*Mephitis* spp.), badgers (*Taxidea taxus*), domestic cats, mountain lions (*Felis concolor*), lynx (*Felis lynx*), and bobcats (*F. rufus*).

Linhart and Knowlton's technique was modified by Lindzey et al. (1977) to index black bear numbers in southwestern Washington. Their results indicated that the scent-station technique was a feasible means of indexing black bear abundance.

Roadside Counts

Roadside counts have long been a standard procedure for obtaining trend indexes in upland game. Roads are traveled for the specific purpose of counting the numbers of individuals of the species being censused which are then related to the number of miles traveled (Overton 1971).

An advantage of this method is that large areas are quickly and easily traversed in an automobile. However, factors affecting the roadside count include (1) activity of the animals as affected by hour of day, food supply, and weather, and (2) condition of the roadside cover. Activity may vary temporally, seasonally, and selectively. In addition, seasonal changes in cover use exist. The tall vegetation of late summer seriously impedes vision; the snow cover of the late winter enhances it (Davis and Winstead 1980).

Miscellaneous Indexes

Reid et al. (1966) investigated a method for approximating pocket gopher (*Thomomys* spp.) populations in western Colorado by counting new signs (mound and earth plugs) on high-altitude livestock ranges. New signs appearing in a 2-day interval and numbers of pocket gophers were counted on 54 plots (40,000 square feet each), during the successive fall seasons. There was a significant, positive correlation between the numbers of pocket gophers, determined by an intensive trapout of each plot, and the number of new signs appearing in the 2-day interval.

McCaffery (1973) showed that the number of white-tailed deer killed by traffic provides a useful index to changes in deer populations in Wisconsin. Road-kill trends correlated extremely well with trends in registered buck harvests. McCaffery concluded that only two ingredients are needed for a road-kill index: accurately reported road-kills and an estimate of percent change in annual traffic volume.

Gunson (1979) studied the use of spotlights to count deer. White-tailed deer and mule deer were counted during fall, on permanent transects, along secondary roads. The source of light was two, 200,000-candle-power aircraft landing lights mounted on the roof of a pickup truck. The driver and one observer each handled a light in a continuous operation on each side of the road. All observed deer were tallied, regardless of distance from vehicle. The preliminary results reported in this study suggested that prehunting season counts of deer on permanent routes could serve as a useful index.

CAPTURE-RECAPTURE METHODS

Typically, in a capture-recapture study, the population is sampled two or more times. Each time, every unmarked animal caught is uniquely marked. Previously marked animals have their recaptures recorded, and then most or all of the animals are released back into the population.

Otis et al. (1978) classified capture studies by two schemes that are directly related to the class of models that are appropriate and the parameter that can be estimated. The first classification addresses the subject of closure—models can be classified as either open or closed. In closed models, the size of a population is constant over the period of investigation. White et al.[5] subdivide the concept of closure into two components: (1) "geographic" closure (i.e., a boundary to limit the population), and (2) "demographic" closure to birth, immigration, death, and emigration.

The distinction between geographic and demographic closure is important, because open models can be subject only to demographic closure; geographic closure is still necessary.[5]

The second classification relates to the type of data collected. Two distinct types of information are provided: (1) information from the recovery of marked animals, and (2) information from comparing numbers of marked and unmarked animals captured at each sampling time.

Data from (1) can be used to estimate survival rates, whereas data from (1) and (2) both are necessary to estimate population size (Pollock 1980).

Otis et al. (1978) presented a review of the chronological development of conceptual approaches to capture-recapture and related experiments. They make it clear that any capture-recapture experiment requires that the researcher make specific assumptions concerning the many factors that affect the results of the experiment. The assumptions that are chosen determine which statistical estimation procedures should produce the best results from the data.

Pollock (1980) stated that the study design for studies of closed populations should be oriented around satisfaction of as many model assumptions as practically possible, so that a simple and reasonably efficient model can be used for estimation of the population. Traditional sample size calculations for a given precision, he noted, are only partially useful, because often the biologists must do a substantial amount of model selection after the study is completed.

Although sample sizes may be limited by practical problems, ideally a study should have approximately 10 sampling periods and constant capture probabilities averaging at least 0.2 for the whole study. This enables reasonable identification of the correct model and good precision of the population size estimator under that model (Pollock 1980).

[5] *White, Gary C., David R. Anderson, Kenneth P. Burnham, and David L. Otis. 1982. Capture-recapture and removal methods for sampling closed populatons. Proposed for publication as a technical report of the Los Alamos National Laboratory, Los Alamos, N. Mex.*

Closed Populations

The general assumptions for the closed-model, capture-recapture methods are as follows:

1. the population is closed,
2. animals do not lose their marks during the experiment,
3. all marks are correctly noted and recorded at each trapping occasion, and
4. each animal has a constant and equal probability of capture on each trapping occasion. This also implies that capture and marking do not affect the catchability of the animal.

The derivation of the formula associated with this method is introduced in many elementary courses in statistics as the "urn model," in which an urn contains N balls, M of which are black. A sample of C balls is then taken, and the number R, which are black is recorded. When an investigator is given M, C, and R and asked to estimate N, this variation leads to the Petersen-Lincoln Index estimator (Overton 1971).

Seber (1973) provided examples of the applications of the Petersen-Lincoln method to populations of underground ants (*Lasius flavus*) (Odum and Pontin 1961); snowshoe hares (*Lepus americanus*) (Green and Evans 1940); climbing cutworms (Wood 1963); redpolls (*Acanthis linaria*) (Nunneley 1964); and roe-deer (*Capreotus capreolus* L.) (Andersen 1962).

Otis et al. (1978) provide a unified approach to estimating parameters in capture-recapture experiments, which includes a statistical testing algorithm that allows the data to aid in selection of the "best" set of assumptions for the experiment. Although assumptions 1-3 must be made for all models considered, the focal point of their models and estimators is to relax assumption 4—equal catchability. They present a sequence of models each allowing for different combinations of up to three types of unequal capture probabilities: (1) capture probabilities vary with time or trapping occasion, (2) capture probabilities vary due to behavioral responses, and (3) capture probabilities vary by individual animal.

Otis et al. (1978) have developed a comprehensive computer program, CAPTURE, to compute estimates and test statistics for the various methods covered in their monograph.

It is appropriate at this point to compare the population estimates obtained through such state-of-the-art analytical aids with those derived from other closed population capture-recapture techniques routinely being practiced. Mares et al. (1981) tested the reliability of estimates obtained from several capture-recapture techniques (Lincoln-Petersen, Schnabel, and Schumacher-Eschmeyer methods) and the Least Squares Removal Method on a known population of eastern chipmunks (*Tamias striatus*). The population was composed of 82 individuals of known age and sex which were released on a 9.4-ha island previously devoid of chipmunks. With the exception of equal catchability, the experiment was designed to satisfy the assumptions of the above methods.

Point estimates always underestimated the true population size, and only the confidence intervals of the Lincoln-Petersen Method consistently included the actual population value. Least squares regression analyses suggested that the experimental population was composed of two groups of animals: those easily trapped and those hesitant to enter traps. As such, all population estimation methods estimated the easily captured portion of the population and underestimated the true size of the population.

In their conclusions, Mares et al. (1981) stated the need to develop estimation techniques that incorporate variable trap response by animals. Although the data necessary to execute the testing and model selection procedures included in program CAPTURE were not available in Mares et al. (1981), these authors indicated that they believed heterogeneity in capture probabilities was the important factor operating in their chipmunk population. Otis et al.[6], therefore, calculated a population estimate based on a model corresponding to such an assumption (Burnham and Overton 1979). The estimate obtained was identical to the known chipmunk population size, indicating the potential of an approach that allows choice of a model appropriate for a given experiment.

Open Populations

When live trapping is conducted over long time periods relative to the population dynamics of the target species, then "open" models become appropriate. In such studies, animals will be both leaving the study area (dying or emigrating) and entering it (being born or immigrating).

A tag-recapture experiment is conducted during which, on successive occasions, animals are captured from the population. The identity of marked individuals (or at least their recapture history) is recorded, unmarked animals are marked, and all (or some) animals are returned to the population. It is assumed that there are losses and additions to the population between occasions, so that there are three parameters of interest on each occasion.

Open models have a varying population size on each capture occasion and also involve survival and recruitment rates for each capture occasion. Burnham (1980) described the development of open models and discussed the steps used to determine capture probabilities. Cormack (1972, 1973) provides good supplementary explanations of the resultant Jolly-Seber model (Jolly 1965, Seber 1965).

Seber (1973) included assumptions for using this model.

1. Every animal in the population, whether marked or unmarked, has the same probability of being caught in successive samples, given that it is alive and in the population when the samples are taken.

[6] *Personal communication from Kenneth P. Burnham, Team Biometrician, Western Energy and Land Use Team, U.S. Fish and Wildlife Service, Fort Collins, Colo.*

2. Every marked animal has the same probability of surviving from the i^{th} to the $(i + 1)^{th}$ sample and of being in the population at the time of the i^{th} sample, given that it is alive and in the population immediately after the i^{th} release. Burnham[8] adds that this assumption is also applicable to the "unmarked" animals or to an estimate of survival from marked animals applied to the whole population.
3. Every animal caught in the i^{th} sample has the same probability of being returned to the population.
4. Marked animals do not lose their marks, and all marks are reported on recovery.
5. All samples are instantaneous (i.e., sampling time is negligible).

The multirelease methods considered so far, although providing maximum information about changes in the population, involve much effort. Also, such multiple releases may be impractical or uneconomical, particularly in the study of commercially exploited populations.

A serious criticism of the Jolly-Seber model, according to Cormack (1979), is that, by including a separate parameter for each survival and each capture probability, it is too general. Any set of experimental observations contains a fixed and limited quantity of information about the system. The more parameters there are in the model, the more thinly the information is spread over them. The consequence with the Jolly-Seber model is that estimates are often found to have variances so large as to render them useless in practice.

A very important new development in open population models is the work of Jolly (1979).[7] He reduced the large number of parameters by assuming a constant survival rate and/or a constant capture rate over the whole study. If these assumptions are realistic, the estimators are much more precise. Crosbie (1979) also considered these models, and developed a computer package to facilitate their use (Pollock 1980).

In the ecological literature, work is only beginning on a log-linear approach to open models (Cormack 1979).

Arnason and Baniuk (1980) discuss a computer system (POPAN) for capture-recapture data obtained from open populations and where marked animals are individually identifiable and classified according to various attributes (age, sex, species, etc.). The system edits and displays the data, provides general statistics-gathering capabilities, and provides a comprehensive set of analyses based on the Jolly-Seber models. Simulations by the system can help in planning experiments and in exploring sources of bias.

There has been an increasing opinion among modelers that "ball and urn models" are not applicable to real biological populations.[8] This is because (1) capture probabilities vary in real populations because of differences in individuals and their responses to previous capture, and (2) there is no analogy in biological populations to the sides of the urn. This lack of analogy creates difficulties in interpreting what N means.

If closure is not true when using closed models, then substantial bias can result in estimating N. If, upon testing, the closure assumption is rejected, then an open model or partially open model may be preferable. However, more research is needed on these models.

REMOVAL METHODS

One way to avoid problems associated with variation in capture probabilities caused by behavioral response is to use a removal model estimator. In removal methods, only the first capture of an individual is used as a basis for estimation.[8]

In a removal study, in contrast to a capture-recapture study, animals are captured and removed from the population instead of being marked and released. On the second and subsequent visits, more animals are captured and removed. Continued sampling would catch progressively fewer animals on each occasion; eventually none would remain to be captured. The progressive decrease in captured animals is used to estimate the total number of animals. Alternatively, the marked animals can be released back into the population. In this way, they are "removed" from the unmarked population without having to physically remove them. This permits capture-recapture experiments to be used as if they were removal experiments.[5]

A hazard of removal studies is that they disrupt the population, and as substantial numbers of animals are removed, immigration may occur, violating the assumption of closure. Live trapping studies can minimize this violation if substantial mortality can be avoided (Otis et al. 1978).

Removal may be by killtrapping, electrofishing, trawling, or merely livetrapping the animals and physically displacing them to another area.

Conducting a removal experiment for purposes of estimating population size may sometimes prove more feasible than a capture-recapture approach. In such cases, the experimenter has available two classes of estimation procedures—the catch-effort techniques usually associated with Leslie and Davis (1939) and DeLury (1947) or the "removal" techniques first introduced by Moran (1951), refined by Zippin (1956, 1958), and generalized by Otis et al. (1978).

Otis et al. (1978) believed that their generalized removal method provides a better approach to estimating the size of a population than do catch-effort techniques, either because of the assumptions involved with the latter or because the concept of effort may be meaningless in many experimental situations. They warned, however, that the operating characteristics of the removal method are not completely satisfactory.

Removal methods are a special case of livetrapping methods; therefore, removal estimators can be used on livetrapping data. Otis et al. (1978) recommended that

---

[7] *Jolly, G. M. Agricultural Research Council Unit of Statistics, University of Edinburgh, Edinburgh, United Kingdom. Mark-recapture models with parameters constant in time. Proposed for publication in Biometrics.*

[8] *Burnham, Kenneth P. Mark-recapture techniques for estimating animal populations—what has been done in ecology. Presented at the U.S. Department of Justice's special workshop: Research methodology in criminal justice program evaluation, March 16-19, 1980. Baltimore, Md.*

livetrapping methods be used, if possible, because of the wider array of options available for the data analysis.

Population Density Estimation

The capture-recapture and removal models discussed involve only population size N as the parameter of interest. However, there may be interest in population density—the number of animals per unit area. To obtain true density values, the area that is being sampled has to be determined. Studies which have used the area enclosed by the sampling grid for population density estimation have resulted in severe overestimation. Such bias results from what has been called "edge effect" (i.e., not all animals have their entire home range within the trapping grid) (Otis et al. 1978).

Metzgar (1972) stated that the investigator seldom knows with certainty the true shape of home ranges sampled by means such as live-trapping or periodic observation. The locations at which the animals are recorded vary with the true shape of the home range, the way activity is distributed within the home range, the number of location records obtained, and the techniques for gathering these records.

Several approaches are given in the biological literature to solve this problem. Dice (1938) suggested that the area actually sampled by a grid of traps could be estimated by adding a strip around the grid equal in width to one-half the width of the home range of the species being censused. This is a good estimate of area sampled only if the grid is a neutral factor in the animals' environment. If the animals are attracted or repelled by the grid, the actual area sampled may not be directly related to size of their home ranges (Swift and Steinhorst 1976).

Two practical ideas for estimating unit area were discussed by Smith et al. (1971). The first involves marking the bait during a prebaiting period to determine the area in which captured animals were feeding prior to the beginning of removal (Adamczyk and Ryzkowski 1968, Gentry et al. 1971). The other method involves the use of assessment lines (e.g., Wheeler and Calhoun 1968).

The use of assessment lines is the most complex approach to population density estimation. Wheeler and Calhoun (1967), in designing a small-mammal census program, International Census of Small Mammals (ICSM), discussed the use of assessment lines to determine the area affected by a grid of traps or an octagon-shaped trap line. These lines extend from the census area into the border zone and are used to estimate the area actually sampled by the census grid or line. There should be some ambient rate (number per unit of linear distance) of catching marked animals along the assessment line. This rate should be a partial function of density, which in turn is determined in the border zone around the census grid or line by the effect of trapping on the census grid or line. The distances at which the rates of capture change will indicate the extent of the area of effect around the grid or line (Smith et al. 1971).

Gentry et al. (1971) tested the ICSM's octagon census method, Category 04 (Wheeler and Calhoun 1967). Early results from the work of Gentry et al. (1971) were instrumental in the designing and testing of a large, modified version of the octagon census method.

Another approach to estimating density has been to combine removal trapping with subsequent trapping on assessment lines to evaluate the area of effect of the original trapping. Smith et al. (1971) combined assessment lines with grid trapping, while Kaufman et al. (1971) trapped first on census lines and subsequently on assessment lines crossing them. In both cases, regression equations relating accumulated captures to distance along the assessment lines within the affected area are used in conjunction with similar regression equations developed from data taken outside the affected area to estimate the proportion of the population removed from the affected area. No objective method for locating the edge of the affected area is provided, however, and that determination will affect the final density estimates. In addition, Gentry et al. (1971) showed that, if there is reinvasion after the original removal, subsequent assessment line trapping may not reveal the limits of the affected area (Swift and Steinhorst 1976).

Spatial relations of the animals may be determined by using outer concentric squares of tightly packed traps (Smith et al. 1971).

Sarrazin and Bider (1973) provided a technique combining removal trapping with an estimate of the resulting decreased activity of the population that yields a density estimate. The technique of estimating population activity by checking fine sand transects for tracks every 2 hours may be too laborious for many applications, however (Swift and Steinhorst 1976).

O'Farrell et al. (1977) described two approaches to estimating the affected area of the trapping configuration from (1) the removal (actual or mathematical) of captured animals (Smith et al. 1971), or (2) captures of marked animals. The first approach assumes a constant population density across the study site, so that the change in the slope of the plot of capture location of unmarked animals delineates the actual area of effect. The same is true for removal trapping using snap traps. The assumption of constant population density also enters into the estimation of the proportion of animals removed from the area of effect for both the removal and mathematical removal procedures, because the average captures per station (or slope) inside the area of effect and the average captures per station (or slope) outside the area of effect are used to estimate the proportion removed. However, the second approach does not assume constant density and can be used only with livetrapping; it delineates the area of effect by means of captures of marked animals along the assessment lines. The ratio of marked animals to total captures adjusts the number of animals marked on the grid or census lines to include those animals that utilized the affected area.

Most of the available techniques for estimating population density have been developed for use with removal trapping. Removal trapping tends to alter normal movement patterns and necessarily obviates following a given population through time. The assessment line technique is applicable to livetrapping and should work better than removal trapping (O'Farrell et al. 1977).

A live-trapping technique for population density estimation of small-mammal populations was described by O'Farrell et al. (1977). Two basic trapping configurations were used—a grid with assessment lines and two parallel census lines with assessment lines. An examination by O'Farrell and Austin (1978) of the density estimates obtained from each basic configuration shows that the two methods are comparable. They believed that the grid yielded more precise areas of effect because of the greater number of traps in a limited area. The grid also enabled the study of detailed home range movements, spatial relationships, and other aspects of small-mammal community dynamics.

The grid arrangement, however, had several drawbacks. There are more trapping stations, requiring more traps, time, and manpower. A grid with assessment lines yields the most information but represents such a major commitment in materials and labor that the ability to study replicate plots simultaneously is severely limited.

Census lines with assessment lines, in contrast yield the basic population measurements using less material and labor. Because this configuration requires less time and effort to establish, several replicate plots can be monitored simultaneously. If replicate plots are sampled within one habitat type, then mean densities and confidence intervals can be calculated (O'Farrell et al. 1977). If density is the measurement goal, they recommended the census line configuration, because it will yield values comparable to those obtainable by the more costly and time consuming grid arrangement.

Otis et al. (1978) advocate an approach to population density estimation for use with grid trapping which formulates the problem as one of joint estimation of density and strip width from data on one sufficiently large grid. Then, by denoting two or more subgrids of different sizes, those parameters can be estimated with a weighted, nonlinear, least squares procedure. This method requires much data to achieve satisfactory results. Both a large trapping grid and many captures are required. A carefully designed study is required to obtain reliable values of density and strip width; only rarely can a typical capture-recapture study be made to yield reasonable results.

CATCH-EFFORT METHODS

Catch-effort methods are based on the general assumption that the size of a sample caught from a population is proportional to the effort put into taking the sample. This means that one unit of sampling effort is assumed to catch a fixed proportion of the population, so that, if samples are permanently removed, the decline in population size will produce a decline in catch per unit effort. Such techniques, first used in 1914 for bears in Norway (Hjort and Ottestad 1933), are now widely used in the study of fish and small-mammal populations, where effort is usually measured in such units as lines or traps per unit time (Seber 1973).

The following assumptions are associated with these techniques (Seber 1973, Davis and Winstead 1980):

1. The population is closed.
2. All individuals have the same probability of being caught during the period of collection of data.
3. The catch is proportional to the population. It is not a strict proportionality, except for short time periods over small amounts of effort. Rather, in general, catch is proportional to $Ne^{-(q \text{ effort})}$.

Ricker (1975) took exception to the first assumption listed above in regard to single homogenous fish populations. In this situation, he stated that when effort is proportional to rate of fishing, the catch per unit effort is proportional to the mean stock present during the time fishing takes place, whether or not recruitment from younger sizes takes place during that time. If the catch can be classified by size (i.e., age cohorts), then assume closure of exploited cohorts. Recruitment into nonexploited cohorts is irrelevant.

Ricker (1975) identified the following systematic errors in catch-effort methods:

1. Many populations have been found not to be amenable to this treatment, either because catchability varies with seasonal changes in environmental conditions or the animal's reactions, or because individual animals differ in vulnerability.
2. There may be day-to-day or other short term variation in catchability.
3. Recruitment and natural mortality, or immigration and emigration, can introduce serious error into these calculations, unless opposed tendencies happen to be in balance.

Ricker (1975) discussed the use of marked populations to check for significant departures from the conditions required for catch-effort estimates.

Dupont (1976) developed a catch-effort model which provides estimates of populations which are superior in accuracy to other catch-effort estimates to date. The assumptions underlying this model are:

1. The population can be divided into distinct cohorts.
2. The relative effort exerted at time t to catch members of a specific cohort is known. The probability that an animal from that cohort will be caught in a small time interval is proportional to Δt, to the effort exerted at time t, and to the cohort size at time t.
3. Some estimate of the cohort survival curves are available.
4. The probability of two or more deaths occurring in the interval is negligible compared to the probability of one death occurring in the same interval.
5. The catch from each cohort in successive time intervals is known.
6. The catches from different cohorts are independent. The probability of obtaining a given catch from any given cohort is unaffected by knowledge about the catch from other cohorts.

This method is designed for populations satisfying these assumptions or conditions: (1) heavy exploitation by man or other predators; (2) the ages of individuals can be readily determined, and (3) some life-table information is known or readily available.

A computer program has been written to perform the computations inherent with this model.

Catch-effort methods are widely used to assess fish stocks around the world. When considering any fish-catching method as a sampling device, it is essential to know how effective the fishing gear is with respect to the quantity of fish caught and how closely the composition of the catch agrees with the composition of the stock. Variations in fish behavior and environment conditions present also cause differences in the efficiency of fishing gear used for sampling (EIFAC 1975).

The yield from traditional gear can be considerably increased by electrification. Electric fishing gear may serve to guide fish into traps, or the electrotoxic or tetanic effects of electric current can be used to capture the fish in some form of auxiliary fishing apparatus (EIFAC 1975).

The cost of collecting catch-effort data is often far less than that for comparable mark-release data. This is because species for which catch-effort data are obtainable are often already being exploited for commercial gain (or pest control). Thus to obtain catch-effort data, it is only necessary to record the activities of the harvester. Also, the problems which arise from the interactions between the observed animals and the data collectors (e.g., trap shyness, trap happiness) are considerably less serious for catch-effort methods than for capture-recapture ones (DuPont 1976).

Creel Census

In this technique, an enumerator roves through the fishing area interviewing anglers to determine the number n of fish caught and the time t expended. The interviewer is assumed to (1) start the trip at a randomly chosen point along a well-defined route which completely covers the fishery, (2) choose the initial direction at random from the two alternatives, and (3) travel at a constant rate of c circuits per day. If the catch rate n/t at time of interview is an unbiased estimator of an angler's catch rate for his completed trip, and, if the angler's movements relative to the interviewer's path never exceed the interviewer's rate c, then rn/ct, summed over all interviews, is an unbiased estimator of the day's total catch. The unit of time is one day, r is the number of times the angler was interviewed, and n/t is the catch rate at the r^{th} interview (Robson 1961).

Some distinctive features of the roving creel census are (1) the open end to the sample—the number of interviews in the sample depends upon the number and distribution of anglers present; (2) the sample of anglers obtained by following some rational route through the fishery constitutes a systematic rather than a random sample; (3) the probability of interviewing any given angler depends in some manner upon how long he fishes; and (4) only incomplete information is obtained for any one angler (Robson 1961).

The major weakness of the roving creel census is that the bias of estimation depends on the basic nature of the random fishing process, which generally is unknown. Unbiasedness of n/t implies that the waiting times to first catch and from first to second catch are identically distributed chance variables, and that all waiting times between successive catches have the same expected value. A variety of arguments could be made for unequal expected waiting times in violation of these conditions for unbiasedness, and the resulting bias could be of considerable magnitude. Robson (1961) suggested several ways of avoiding or minimizing this problem by making the creel census distribution-free, in the sense of an ordinary sample survey method.

Malvestuto et al. (1978) concluded that the roving creel method was sensitive enough to detect the size of changes in the quality of fishing in which managers were interested.

CHANGE-IN-RATIO METHOD

This technique basically requires a conceptual splitting of the population of interest into two exclusive and exhaustive components, using some criterion, such as sex or age class (e.g., juvenile or adult). Knowledge of the change in proportion or ratio of the two components before and after a known number of additions to, or removals from, each component specifies the initial size of each component. By sampling the population before and after the known additions or removals are made and obtaining estimates of the before and after proportions, estimates of the size of the population components (and hence total population size) can be produced (Otis 1980).

The following assumptions are made when using the CIR method:

1. Mortality rates for members of all disjoint components are the same.
2. All members of the population have the same probability of being sampled in each of the preremoval and postremoval samples.

Paulik and Robson (1969) discussed change-in-ratio (CIR) estimators for population abundance, productivity, and exploitation rates, and survival characteristics from observed changes in population composition.

Occasionally, an investigator is unable to classify correctly a significant proportion of the population into one of the two components originally conceptualized. For example, the researcher may originally intend to classify the animals in the preremoval and postremoval samples as either male or female. If the sampling is done by observing animals from a great distance, such as in aerial sampling, then it may be impossible to classify the young of the year accurately by sex. In this instance, categorizing the animals as either male, female, or juvenile (three disjoint components) would be more desirable. Otis (1980) presented a method for producing maximum likelihood estimates of each of the three population components in sampling experiments.

BOUNDED COUNTS METHOD

Regier and Robson (1967) suggested the following "bounded counts" method, based on the theory of Robson and Whitlock (1964). The underlying assumptions for using this method are that repeated counts are possible and that no units are counted twice.

Let N be the true number of units, and let N_m, N_{m-1} be the largest and the second largest counts obtained, respectively. Then N can be estimated by

$$\hat{N} = N_m + (N_m - N_{m-1}) = 2N_m - N_{m-1} \qquad [3]$$

and an approximate 100% (1-a) confidence interval for N is

$$N_m < N < [N_m - (1\text{-}a)N_{m-1}]/a. \qquad [4]$$

If s independent counts are made, then the bias of $\hat{N}$ is of order $1/s^2$. For cases when more than two counts are made, Robson and Whitlock (1964) derived further corrections to reduce the bias (Seber 1973).

Seber (1973) suggested that this method could be applied in counting migrating fish-runs from a number of vantage points by equally perceptive enumerators or mechanical devices, and in small ponds, through which sieves may be drawn at least twice during an interval, when the population is closed.

LITERATURE CITED

Adamczyk, Krystyna, and Lech Ryszkowski. 1968. Estimation of the density of a rodent population using stained bait. Acta Theriologica 13(17):295-311.

Andersen, J. 1962. Roe-deer census and population analysis by means of modified marking and release technique. p. 72-82. *In* The exploitation of natural animal populations. E. D. LeCren and M. W. Holdgate, editors. Blackwell, Oxford, England.

Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, Ill.

Arnason, A. Neil, and Leonard Baniuk. 1980. A computer system for mark-recapture analysis of open populations. Journal of Wildlife Management 44(2): 325-332.

Batcheler, C. L., and D. J. Bell. 1970. Experiments in estimating density from joint point- and nearest-neighbor distance samples. New Zealand Ecological Society Proceedings 17:111-117.

Best, Louis B. 1975. Interpretational errors in the "mapping method" as a census technique. Auk 92(3): 452-460.

Blankenship, Lytle H., Alan B. Humphrey, and Duncan MacDonald. 1971. A new stratification for mourning dove call-count routes. Journal of Wildlife Management 35(2):319-326.

Braun, Clait E., Raymond K. Schmidt, and Glenn E. Rogers. 1973. Census of Colorado white-tailed ptarmigan with tape-recorded calls. Journal of Wildlife Management 37(1):90-93.

Brown, David E., and Ronald H. Smith. 1976. Predicting hunting success from call-counts of mourning and white-winged doves. Journal of Wildlife Management 40(4):743-749.

Brown, David E., Collins L. Cochran, and Thomas E. Waddell. 1978. Using call-counts to predict hunting success for scaled quail. Journal of Wildlife Management 42(2):281-287.

Buckley, P. A., and F. Buckley. 1976. Guidelines for protection and management of colonial nesting water birds. 54 p. U.S. National Park Service, North Atlantic Regional Office, Boston, Mass.

Buechner, H. K., I. O. Buss, W. M. Longhurst, and A. C. Brooks. 1963. Numbers and migration of elephants in Murchison Falls National Park, Uganda. Journal of Wildlife Management 27(1):36-53.

Burnham, Kenneth P., and W. Scott Overton. 1979. Robust estimation of population size when capture probabilities vary among animals. Ecology 60(5): 927-937.

Burnham, Kenneth P., David R. Anderson, and Jeffrey L. Laake. 1980. Estimation of density from line transect sampling of biological populations. 202 p. Wildlife Monograph 72.

Caughley, Graeme. 1974. Bias in aerial survey. Journal of Wildlife Management 38(4):921-933.

Cochran, William G. 1977. Sampling techniques. Third edition. 428 p. John Wiley and Sons, New York, N.Y.

Cormack, R. M. 1972. The logic of capture-recapture estimates. Biometrics 28(2):337-343.

Cormack, R. M. 1973. Commonsense estimates from capture-recapture studies. p. 225-235. *In* The mathematical theory of the dynamics of biological populations. M. S. Bartlett and R. W. Hiorns, editors. Academic Press, London, England.

Cormack, R. M. 1979. Models for capture-recapture. p. 217-255. *In* Sampling biological populations. Richard M. Cormack, Ganapati P. Patil, and Douglas S. Robson, editors. 392 p. International Cooperative Publishing House, Fairland, Md.

Croon, Gale W., Dale R. McCullough, Charles E. Olson, Jr., and Leland M. Queal. 1968. Infrared scanning techniques for big game censusing. Journal of Wildlife Management 32(4):751-759.

Crosbie, S. F. 1979. The mathematical modelling of capture-mark-recapture experiments on open animal populations. Ph.D. dissertation. University of Otago, Dunedin, New Zealand.

Davis, David E., and Ray L. Winstead. 1980. Estimating the numbers of wildlife populations. p. 221-245. *In* Wildlife management techniques manual. S. D. Schemnitz, editor. 686 p. The Wildlife Society, Washington, D.C.

Dawson, David G. 1981. The usefulness of absolute (census) and relative (sampling or index) measures of abundance. p. 554-558. *In* Estimating numbers of terrestrial birds. C. John Ralph and J. Michael Scott, editors. Studies in Avian Biology 6. Allen Press, Lawrence, Kans.

DeLury, D. B. 1947. On the estimation of biological populations. Biometrics 3(4):145-167.

Dice, Lee R. 1938. Some census methods for mammals. Journal of Wildlife Management 2(3):119-130.

Diggle, P. J. 1975. Robust density estimation using distance methods. Biometrika 62:39-48.

Diggle, Peter J. 1979. Statistical methods for spatial point patterns in ecology. p. 95-150. In Spatial and temporal analysis in ecology. R. M. Cormack and J. K. Ord, editors. 356 p. International Cooperative Publishing House, Fairland, Md.

Dupont, D. W. 1976. A stochastic method for estimating animal abundance from catch-effort data. Ph.D. dissertation. Johns Hopkins University, Baltimore, Md.

Eberhardt, L. L. 1978a. Appraising variability in population studies. Journal of Wildlife Management 42(2): 207-238.

Eberhardt, L. L. 1978b. Transect methods for population studies. Journal of Wildlife Management 42(1):1-31.

Eberhardt, L. L., D. G. Chapman, and J. R. Gilbert. 1979. A review of marine mammal census methods. 46 p. Wildlife Monographs 63.

Eltringham, S. K. 1973. An assessment of variability in repeated ground counts of large African mammals. Journal of Applied Ecology 10(2):409-415.

Emlen, John T. 1971. Population densities of birds derived from transect counts. Auk 88(2):323-342.

Erickson, Albert W., and Donald B. Siniff. 1963. A statistical evaluation of factors influencing aerial survey results on brown bears. Transactions of the North American Wildlife and Natural Resources Conference 28:391-409.

European Inland Fisheries Advisory Commission, Food and Agricultural Organization of the United Nations. 1974. Report of the symposium on the methodology for the survey, monitoring and appraisal of fishery resources in lakes and large rivers. 33 p. [Aviemore, Scotland (U.K.), May 2-4, 1974] EIFAC Technical Paper 23. Food and Agriculture Organization of the United Nations, Rome, Italy.

Fenneman, Nevin M. 1938. Physiography of eastern United States. First edition. 714 p. McGraw-Hill Book Company, New York, N.Y.

Fenneman, Nevin. 1931. Physiography of western United States. First edition. 534 p. McGraw-Hill Book Company, New York, N.Y.

Ferris, Craig R. 1979. Effects of Interstate 95 on breeding birds in northern Maine. Journal of Wildlife Management 43(2):421-427.

Floyd, Theodore J., L. David Mech, and Michael E. Nelson. 1979. An improved method of censusing deer in deciduous-coniferous forests. Journal of Wildlife Management 43(1):258-261.

Franzmann, Albert W., Paul Arneson, and John L. Oldemeyer. 1976. Daily winter pellet groups and beds of Alaskan moose. Journal of Wildlife Management 40(2):374-375.

Gates, Charles E. 1979. LINETRAN—User's Guide. 33 p. Texas A and M University, College Station.

Gates, Charles E. 1980. LINETRAN, a general computer program for analyzing line-transect data. Journal of Wildlife Management 44(3):658-661.

Gates, Charles E., William H. Marshall, and David P. Olson. 1968. Line transect method of estimating grouse population densities. Biometrics 24(1):135-145.

Gates, Charles E., Ted L. Clark, and Kenneth E. Gamble. 1975. Optimizing mourning dove breeding population surveys in Texas. Journal of Wildlife Management 39(2):237-242.

Gentry, John B., Michael H. Smith, and John G. Chelton. 1971. An evaluation of the octagon census method for estimating small mammal populations. Acta Theriologica 16:149-159.

Graves, H. B., E. D. Bellis, and W. M. Knuth. 1972. Censusing white-tailed deer by airborne thermal infrared imagery. Journal of Wildlife Management 36(3): 875-884.

Green, R. G., and C. A. Evans. 1940. Studies on a population cycle of snowshoe hares on the Lake Alexander area. I: Gross annual censuses, 1932-1939. Journal of Wildlife Management 4(2):220-238.

Gunson, John R. 1979. Use of night-lighted census in management of deer in Alberta and Saskatchewan. Wildlife Society Bulletin 7(4):259-267.

Hein, Dale. 1965. Wood duck roosting flight phenomena. Ph.D. thesis. Iowa State University, Ames.

Hein, Dale, and Arnold O. Haugen. 1966. Autumn roosting flight counts as an index to wood duck abundance. Journal of Wildlife Management 30(3):657-668.

Hirsch, Allan, William B. Krohn, Dennis L. Schweitzer, and Carl H. Thomas. 1979. Trends and needs in federal inventories of wildlife habitat. Transactions of the North American Wildlife and Natural Resources Conference 44:340-359.

Hjort, J. G., and P. Ottestad. 1933. The optimum catch. Hvalraadets Skrifter Oslo 7:92-127.

Husch, Bertram, Charles I. Miller, and Thomas W. Beers. 1972. Forest mensuration. Second edition. 410 p. The Ronald Press Co., New York, N.Y.

International Bird Census Committee. 1970. Recommendations for an international standard for a mapping method in bird census work. Audubon Field Notes 24(6):722-726.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration—stochastic model. Biometrika 52, 225-47.

Jolly, G. M. 1979. A unified approach to mark-recapture stochastic models, exemplified by a constant survival rate model. In Sampling biological populations. Statistical Ecology. Volume 5. R. M. Cormack, G. P. Patil, and D. S. Robson, editors. International Cooperative Publishing House, Fairland, Md.

Kaufman, Donald W., Gary C. Smith, R. Marie Jones, John B. Gentry, and Michael H. Smith. 1971. Use of assessment lines to estimate density of small mammals. Acta Theriologica 16:127-147.

Kendall, Maurice G., and P. A. P. Moran. 1963. Geometrical probability. 125 p. Griffin's Statistical Monographs and Courses 10. Griffin, London, England.

Küchler, August W. 1964. Manual to accompany the map: Potential natural vegetation of the conterminous United States. 116 p. American Geographical Society of New York Special Publication 36. New York, N.Y.

Kushlan, James A. 1979. Effects of helicopter censuses on wading bird colonies. Journal of Wildlife Management 43(3):756-760.

Laake, J. L., Kenneth P. Burnham, and David R. Anderson. 1979. User's manual for program TRANSECT. 26 p. Utah State University Press, Logan.

Lavigne, D. M., and N. A. Oritsland. 1974. Ultraviolet photography: A new application for remote sensing of mammals. Canadian Journal of Zoology 52(7):939-941.

Lavigne, David M., S. Innes, K. Kalpakio, and K. Ronald. 1975. An aerial census of western Atlantic harp seals (*Pagophilus groenlandicus*) using ultraviolet photography. International Commission for the Northwest Atlantic Fisheries Research Document 75/XII/144.

Leopold, A. Starker, Thane Riney, Randall McCain, and Lloyd Teirs, Jr. 1951. The Jawbone deer herd. Game Bulletin 4. 136 p. California Division of Fish and Game, Sacramento, Calif.

Leslie, P. H., and D. H. S. Davis. 1939. An attempt to determine the absolute number of rats on a given area. Journal of Animal Ecology 8:94-113.

Lewis, James C. 1970. Wildlife census methods: A resume. Journal of Wildlife Diseases 6(4):356-364.

Lindzey, Frederick G., Steven K. Thompson, and John I. Hodges. 1977. Scent station index of black bear abundance. Journal of Wildlife Management 41(1):151-153.

Linhart, Samual B., and Frederick F. Knowlton. 1975. Determining the relative abundance of coyotes by scent station lines. Wildlife Society Bulletin 3(3):119-124.

Malvestuto, Stephen P., William D. Davies, and William L. Shelton. 1978. An evaluation of the roving creel survey with nonuniform probability sampling. Transactions of the American Fisheries Society 107(2): 255-262.

Mares, M. A., K. E. Streilein, and M. R. Willig. 1981. Experimental assessment of several population estimation techniques on an introduced population of eastern chipmunks. Journal of Mammology 62(2):315-328.

Marion, Wayne R., Timothy E. O'Meara, and David S. Maehr. 1981. Use of playback recordings in sampling elusive or secretive birds. p. 81-85. *In* Estimating numbers of terrestrial birds. C. John Ralph and J. Michael Scott, editors. Studies in Avian Biology 6. Allen Press, Lawrence, Kans.

Martin, Fant W., Richard S. Pospahala, and James D. Nichols. 1979. Assessment and population management of North American migratory birds. p. 187-239. In Environmental biomonitoring, assessment, prediction, and management—certain case studies and related quantitive issues. John Cairns, Jr., Ganapati P. Patil, and William E. Waters, editors. 450 p. International Co-operative Publishing House, Fairland, Md.

McCaffery, Keith R. 1973. Road-kills show trends in Wisconsin deer populations. Journal of Wildlife Management 37(2):212-216.

McCaffery, Keith R. 1976. Deer trail counts as an index to populations and habitat use. Journal of Wildlife Management 40(2):308-316.

McIntyre, G. A. 1953. Estimation of plant density using line transects. Journal of Ecology 41(2):319-330.

Metzgar, Lee H. 1972. The measurement of home range shape. Journal of Wildlife Management 36(2):643-645.

Mikol, Sharon A., J. J. Hickey, J. R. Cary, A. K. Stratman, and M. E. Lardy. 1979. Comparison of bird-transect estimators in sagebrush and grassland habitats. p. 1-76. *In* Estimating breeding-bird densities on coal lands in Montana and Wyoming. U.S. Fish and Wildlife Service, Western Energy and Land Use Team Report 79/W3. Fort Collins, Colo.

Mikol, Sharon A. 1980. Field guidelines for using transects to sample nongame bird populations. 26 p. U.S. Fish and Wildlife Service, Biological Services Program Report 80/58. Fort Collins, Colo.

Moran, P. A. P. 1951. A mathematical theory of animal trapping. Biometrika 38:307-311.

Neff, Don J. 1968. The pellet-group count technique for big game trend, census, and distribution: A review. Journal of Wildlife Management 32(3):597-614.

Nichols, Lyman. 1980. Mountain goat management technique studies. 51 p. Alaska Department of Fish and Game, Final Report, Federal Aid in Wildlife Restoration Projects W-17-9, W-17-10, and W-17-11, Jobs 12.2R and 12.3R. Juneau, Alaska.

Norton-Griffiths, M. 1976. Further aspects of bias in aerial census of large mammals. Journal of Wildlife Management 40(2):368-371.

Nunneley, Sarah Ann. 1964. Analysis of banding records of local populations of Blue Jays and Redpolls at Granby, Mass. Bird-Banding 35(1):8-22.

Odum, Eugene P., and A. J. Pontin. 1961. Population density of the underground ant (*Lasuis flavus*) as determined by tagging with P^{32}. Ecology 42(1):186-188.

O'Farrell, Michael J., Donald W. Kaufman, and Dale W. Lundall. 1977. Use of live-trapping with the assessment line method for density estimation. Journal of Mammology 58(4):575-582.

O'Farrell, Michael J., and George T. Austin. 1978. A comparison of different trapping configurations with the assessment line technique for density estimations. Journal of Mammology 59(4):866-868.

Otis, David L. 1980. An extension of the change-in-ratio method. Biometrics 36:141-147.

Otis, David L., Kenneth P. Burnham, Gary C. White, and David R. Anderson. 1978. Statistical inference from capture data on closed animal populations. 135 p. Wildlife Monograph 62.

Overton, W. Scott. 1971. Estimating the numbers of animals in wildlife populations. p. 403-456. *In* Wildlife Management Techniques. Third edition, revised. Robert H. Giles, Jr., editor. 633 p. The Wildlife Society, Washington, D.C.

Parker, H. Dennison, Jr., and Richard S. Driscoll. 1972. An experiment in deer detection by thermal scanning. Journal of Range Management 25(6):480-481.

Parr, Delbert E., and M. Douglas Scott. 1978. Analysis of roosting counts as an index to wood duck population size. Wilson Bulletin 90(3):423-437.

Paulik, G. J., and D. S. Robson. 1969. Statistical calculations for change-in-ratio estimators of population parameters. Journal of Wildlife Management 33(1): 1-27.

Pollock, K. H. 1980. Capture-recapture models: A review of current methods, assumptions and experimental design. 32 p. Institute of Statistics Mimeo Series 1308, North Carolina State University, Raleigh.

Ramsey, Fred L., and J. Michael Scott. 1979. Estimating population densities from variable circular plot surveys. p. 155-181. *In* Sampling biological populations. Richard M. Comack, Ganapati P. Patil, and Douglas S. Robson, editors. 392 p. International Co-operative Publishing House, Fairland, Md.

Reeves, R. G., editor. 1975. Manual of remote sensing. 2 vols. 2,142 p. American Society of Photogrammetry, Falls Church, Va.

Regier, H. A., and D. S. Robson. 1967. Estimating population number and mortality rates. p. 31-66. *In* The biological basis of freshwater fish production. S. D. Gerking. Blackwell Scientific Publications, Oxford, England, and Edinburgh, Scotland.

Reid, V. H., R. M. Hansen, and A. L. Ward. 1966. Counting mounds and earth plugs to census mountain pocket gophers. Journal of Wildlife Management 30(2):327-334.

Ricker, William E. 1975. Computation and interpretation of biological statistics of fish populations. xviii + 382 p. Fisheries Research Board of Canada Bulletin 191.

Robson, D. S. 1961. On the statistical theory of a roving creel census of fishermen. Biometrics 17:415-437.

Robson, D. S., and J. H. Whitlock. 1964. Estimation of a truncation point. Biometrika 51:33-39.

Sarrazin, J-P. Raymond, and J. Roger Bider. 1973. Activity, a neglected parameter in population estimates-the development of a new technique. Journal of Mammology 54(2):369-382.

Schweitzer, Dennis L., Thomas W. Hoekstra, and Charles T. Cushwa. 1981. Lessons from past national assessments of wildlife and fish: Information and coordination needs for the future. Transactions of the North American Wildlife and Natural Resources Conference 46:147-155.

Seber, G. A. F. 1965. A note on the multiple recapture census. Biometrika 52:249-259.

Seber, G. A. F. 1973. The estimation of animal abundance and related parameters. 506 p. Hafner Press, New York, N.Y.

Seber, G. A. F. 1980. Some recent advances in the estimation of animal abundance. 101 p. University of Washington, Division of Marine Resources Technical Report WSG 80-1. University of Washington, Seattle.

Seber, G. A. F. 1981. The estimation of animal abundance and related parameters, Second edition. (In press).

Smith, M. M. 1958. Louisiana wood duck roost counts. 3 p. Wildlife and Fish Commission, New Orleans, La.

Smith, Michael H., Roland Blessing, John G. Chelton, John B. Gentry, Frank B. Golley, and John T. McGinnis. 1971. Determining density for small mammal populations using a grid and assessment lines. Acta Theriologica 16(8):105-125.

Swift, David M., and R. Kirk Steinhorst. 1976. A technique for estimating small mammal population densities using a grid and assessment lines. Acta Theriologica 21:471-480.

Tabberer, D. K., J. D. Newsom, P. E. Schilling, and H. A. Bateman. 1971. The wood duck roost count as an index to wood duck abundance in Louisiana. Proceedings of Southeastern Association of Game and Fish Commissioners 25:254-261.

Wenger, C. R., and A. T. Gringan. 1978. Scien-elicited coyote vocalizations: an evaluation of a census technique. Wildlife Society Bulletin 6(2):73-76.

Wheeler, G. G., and J. B. Calhoun. 1967. Programs and procedure of the International Census of Small Mammals (ICSM). 29 p. U.S. Department of Health, Education and Welfare, National Institute Mental Health, Bethesda, Md. (Mimeo).

Wheeler, G. G., and J. B. Calhoun. 1968. Manual for conducting ICSM census category 04. (Octagon census and assessment traplines). ICSM manual series 4, Parts 1 and 2, Ed. 1:1-50. U.S. Department of Health, Education and Welfare, Bethesda, Md.

Williams, A. B. 1936. The composition and dynamics of a beech-maple climax community. Ecological Monographs 6:317-408.

Winn, H. E., R. K. Edel, and A. G. Taruski. 1975. Population estimate of the humpback whale (*Megaptera novasangliae*) in the West Indies by visual and acoustic techniques. Journal of the Fisheries Research Board of Canada 32(4):499-506.

Wood, G. W. 1963. The capture-recapture technique as a means of estimating populations of climbing cutworms. Canadian Journal of Zoology 41:47-50.

Wride, M. C., and K. Baker. 1977. Thermal imagery for census of ungulates. Proceedings of the International Symposium on Remote Sensing of the Environment 11: 1091-1099.

Zippin, Calvin. 1956. An evaluation of the removal method of estimating animal populations. Biometrics 12(2):163-189.

Zippin, C. 1958. The removal method of population estimation. Journal of Wildlife Management 22:82-90.

☆U.S. GOVERNMENT PRINTING OFFICE: 1984-0-777-733/9146

Miller, Stephen A. 1984. Estimation of animal production numbers for national assessments and appraisals. USDA Forest Service General Technical Report RM-105, 23 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Population inventory methods and associated data are best applied in national assessments of wildlife and fish in conjunction with analytical approaches which utilize estimates of the production capability of the supporting habitat. The state of knowledge in estimating animal population numbers is contrasted with the state of practice. Problems inherent with available population data in regards to their use as input for national assessments are reviewed.

Keywords: Census, inventory, national assessments

Miller, Stephen A. 1984. Estimation of animal production numbers for national assessments and appraisals. USDA Forest Service General Technical Report RM-105, 23 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Population inventory methods and associated data are best applied in national assessments of wildlife and fish in conjunction with analytical approaches which utilize estimates of the production capability of the supporting habitat. The state of knowledge in estimating animal population numbers is contrasted with the state of practice. Problems inherent with available population data in regards to their use as input for national assessments are reviewed.

Keywords: Census, inventory, national assessments

Miller, Stephen A. 1984. Estimation of animal production numbers for national assessments and appraisals. USDA Forest Service General Technical Report RM-105, 23 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Population inventory methods and associated data are best applied in national assessments of wildlife and fish in conjunction with analytical approaches which utilize estimates of the production capability of the supporting habitat. The state of knowledge in estimating animal population numbers is contrasted with the state of practice. Problems inherent with available population data in regards to their use as input for national assessments are reviewed.

Keywords: Census, inventory, national assessments

Miller, Stephen A. 1984. Estimation of animal production numbers for national assessments and appraisals. USDA Forest Service General Technical Report RM-105, 23 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Population inventory methods and associated data are best applied in national assessments of wildlife and fish in conjunction with analytical approaches which utilize estimates of the production capability of the supporting habitat. The state of knowledge in estimating animal population numbers is contrasted with the state of practice. Problems inherent with available population data in regards to their use as input for national assessments are reviewed.

Keywords: Census, inventory, national assessments

U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

Rocky Mountains

Southwest

Great Plains

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

RESEARCH FOCUS

Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

RESEARCH LOCATIONS

Research Work Units of the Rocky Mountain Station are operated in cooperation with universities in the following cities:

Albuquerque, New Mexico
Flagstaff, Arizona
Fort Collins, Colorado*
Laramie, Wyoming
Lincoln, Nebraska
Rapid City, South Dakota
Tempe, Arizona

*Station Headquarters: 240 W. Prospect St., Fort Collins, CO 80526